DISTRIBUTION AND RISK-SENSITIVE FORAGING OF JUVENILE GADIDS IN RELATION TO FRACTAL COMPLEXITY OF EELGRASS (*Zostera marina*) HABITAT

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by

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Abstract

The influence of habitat configuration on faunal distribution and success is largely unknown, despite a large body of literature concerning implications of habitat fragmentation. In Newfoundland coastal waters, a number of juvenile fish species, including Atlantic cod (*Gadus morhua*), are associated with eelgrass (*Zostera marina*), a habitat that naturally occurs in a variety of configurations and that is susceptible to anthropogenic fragmentation. Studies have shown that the strength of this association is variable at different eelgrass sites and across scales. Given this inconsistent association and the complex spatial configurations of eelgrass, I investigated the relationships between a number of spatial characteristics of eelgrass and density of three juvenile (age-0) fish species, Atlantic cod, Greenland cod (*G. ogac*), and white hake (*Urophycis tenuis*). I used data from aerial photographs to determine perimeter and area measurements at multiple scales, fractal dimensions of perimeter (D_P) and area (D_A), and a measure that combines perimeter and area complexity at these scales ($\beta_{P/A}$). Age-0 fish densities were estimated at each eelgrass site using a seine net. I found parabolic relationships between $\beta_{P/A}$ and density for all three species, indicating highest fish densities at sites of intermediate patchiness and edge regularity. Furthermore, I determined that $\beta_{P/A}$ provided a less ambiguous estimate of spatial configuration than other measures. This intermediate maximum may reflect a trade-off, whereby eelgrass sites of intermediate spatial complexity provide juvenile fish with both optimal protective cover and opportunity to feed. I assessed this hypothesis by measuring foraging success in age-0 Greenland cod at sites of varying eelgrass fragmentation, as measured by $\beta_{P/A}$. I found that foraging success depends on cod density. I then combined this relationship and the parabolic relationship between density and fragmentation to develop a model that predicts the observed relationship between foraging success and eelgrass site configuration. My thesis demonstrates that eelgrass habitat configuration influences the density and success of resident fish fauna. Furthermore, this research demonstrates that predictive models are possible in ecology.

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$\beta_{A=f(P)}$ – scaling co-efficient describing how area changes as a function of perimeter
$\beta_{P/A}$ - scaling co-efficient describing how perimeter:area estimates change with scale
μ - mortality rate
A - area
a – co-efficient that describes the degree of vertical (along the y-axis) stretching or compression for a given function
C – index of complexity
c – constant term in a quadratic function
cm - centimetre
D – fish density
D_A – fractal dimension of area
D_P – fractal dimension of perimeter
ESW – empty stomach weight
f – foraging rate
FS (Chapter 2) – Fleming Survey
FS (Chapter 3) – foraging success
FSW - full stomach weight
FW – fish weight
g – growth rate
g -gram
IOH – Intermediate Optimum Hypothesis
km - kilometre
L - length
m - metre
M - month
mm – millimetre
NS – Newman Sound
°C – degrees Celsius
OFT – Optimal Foraging Theory
P - perimeter
P/A – perimeter to area ratio
PC1 – first principle component
PCA – principle component analysis
TW – total weight
x_o - translates a given function along the x-axis
Y – Year

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Chapter 1: Habitat and landscape use in ecology: Applications to the coastal juvenile fish community of Newfoundland.

Many life-history characteristics of animals, including growth, dispersal, and reproduction, as well as the behaviours that influence their success, are influenced by the spatial allocation of resources in heterogeneous landscapes (Turner *et al.* 2001). Habitat and habitat use link multiple ecological disciplines including landscape, population, and behavioural ecology (Pulliam *et al.* 1992, Wiens *et al.* 1993, Lima and Zollner 1996). Additionally, patterns of habitat use have both applied and theoretical importance. From an applied perspective, determining relationships between populations and landscapes has imperative implications for management and conservation efforts (reviewed in Sutherland 1998). In addition, assessing changes in habitat use in response to anthropogenic influences - such as changes in habitat fragmentation - may prove to be a helpful conservation tool and aid in understanding the effects of these human disturbances.

Lima and Zollner (1996) identified a disconnect in the spatial scale of assessment as the primary factor isolating landscape-level ecology from advances in behavioural ecology. In the sections below, I present one explanatory framework for habitat selection and link this framework to usage patterns in complex habitats. Furthermore, I discuss how habitat configuration may influence these patterns and the importance of linking these concepts via a multi-scale approach. In a second section, I introduce the ecological system in which I have studied these interactions.

1.2 Using habitat to balance conflicting demands: Risk/reward trade-offs

Optimal foraging theory (OFT) is comprised of models developed to determine what, when, and where animals eat. Initially, OFT suggested that individuals should forage so that they maximize the rate of energy intake (e.g.Emlen 1966, MacArthur and Pianka 1966, Charnov 1976, Pyke 1984). However, the influences of predation risk and anti-predatory responses on foraging have generated a large body of literature since the conception of OFT (e.g. Milinski and Heller 1978, Sih 1980, Lima and Dill 1990, Lima 1998). To address this ability to balance conflicting demands, the central tenet of OFT is that, given a set of alternative scenarios, an individual will forage in such a way as to maximize the ratio of benefits to costs.

One area in which animals are likely to balance conflicting demands is in their use of space. If habitats differ in their availability of resources and hazards, then conflicts in habitat selection may occur. For example, habitats that provide the maximum opportunity to feed may not provide the maximum amount of shelter from predation. Several studies have demonstrated that foragers will shift habitats in the presence of predators at the cost of a lower foraging rate (e.g. Mittlebach 1981, 1984, Werner *et al.* 1983, Brown 1988, Pierce 1988, Gotceitas 1990). Recognizing that animals often choose between habitats that differ in predation hazard and foraging return, Werner and Gilliam (1984) proposed the "minimize μ/g" rule, which states that individuals should select habitats that provide the smallest risk (measured as mortality rate, μ) for the greatest reward (growth rate, g). Gilliam and Fraser (1987) then tested a variation of this model "minimize μ/f", substituting foraging rate (f) for growth rate.

For many species, risk of predation is heavily influenced by the physical structure of habitat (Lima 1998). The effects of physical structure can be either positive or negative, depending upon the predator-prey system. For example, female Dall sheep (*Ovis dalli dalli*) are more vigilant when foraging near obstructive cover which may conceal the approach of predators than when on open cliffs (Frid 1997). Similarly, some species of desert grassland birds avoid vegetation in the presence of predators (Lima and Valone 1991). Alternatively, many species appear to use physical structure of habitat – or protective cover - to minimize interactions with potential predators (Lima and Dill 1990). This pattern has been observed in fish such as pink salmon fry (*Oncorhynchus gorbuscha* – Magnhagen 1988), bluegill sunfish *Lepomis macrochirus* (Crowder and Cooper 1982, Savino and Stein 1982, Werner *et al.* 1983, Gotceitas and Colgan 1987, 1989), cunner *Tautogolabrus adspersus* (Tupper and Boutilier 1997), and red drum *Sciaenops ocellatus* (Rooker *et al.* 1998). This tactic is also common in invertebrates such as web-building spiders (Bilde *et al.* 2002), larval dragonflies (Pierce 1988), and the American lobster (Spanier *et al.* 1998), birds such as tits (*Parus spp.* - Walther and Gosler 2001), white-crowned sparrows (Lima 1990), and black-capped chickadees (Lima 1985), as well as mammalian species including grey squirrels (Lima *et al.* 1985), guinea pigs (Cassini and Galante 1992), and mule deer (Pierce *et al.* 2004).

1.3 The importance of complex habitat and the role of fragmentation

The influence of structurally complex habitats on resident fauna has been the focus of numerous investigations. Several studies have shown that structurally complex

habitats exhibit increased biodiversity and faunal abundance over unstructured, homogenous habitats. This pattern has been identified in habitats including forests, mangroves, coral reefs, rocky intertidal, and seagrass beds, and species including birds (MacArthur and MacArthur 1961), rodents (Rosenzweig and Winakur 1969), fish (Tonn and Magnuson 1982), and seagrass and rocky shore invertebrates (Kohn and Leviten 1976, Heck and Wetstone 1977, Dean and Connell 1987a, b). A number of possible mechanisms have been suggested to explain this phenomenon. These include an increased number and variety of resources including refuges and food resources (MacArthur and Levins 1967, Orth *et al* 1984, Hicks 1985, O'Connor 1991), which in turn corresponds to an increased number of ecological niches (termed the habitat diversity hypothesis, e.g. Debski *et al.* 2002). Additionally, it has been argued that complex habitats reduce both biotic (e.g. Orth *et al.* 1984, Diehl 1988, Hixon and Menge 1991) and physical (Dean and Connell 1987a) stressors by reducing encounter rates with competitors and predators and reducing exposure to damaging environmental factors.

The availability of complex habitat seems important for the community structure of many ecological systems. However, the effects of spatial arrangement of habitat are less clear despite a large body of literature concerning habitat fragmentation (Debinski and Holt 2000). Fahrig (2003) noted that there is discrepancy in the conceptualization and measurement of this important ecological process. Specifically, she suggested that many studies equate amount of habitat, or loss of habitat, with fragmentation (Fahrig 2003). For example, measures of percent cover, patch size, and patch isolation are often used to assess habitat fragmentation and its effects (Ewers and Didham 2006). Changes

in habitat amount may indicate anthropogenically fragmented habitats. However, fragmentation of habitat per se refers to changes in habitat configuration, independent of amount (Fahrig 2003). Contradiction among fragmentation studies may also result from scale of assessment. These investigations are largely conducted on a patch scale, and therefore, the observed patterns are unlikely to be representative of the effects occurring at the broader landscape scale (see Section 1.4). In addition to concerns of how to quantify the spatial arrangment of habitat, habitat fragmentation and loss are accelerating. Therefore, because of the possible negative effects of habitat fragmentation, the ability to assess how changes in the spatial arrangement of habitat affect fauna – at scales ranging from behavioural mechanisms to community structure – is paramount.

1.4 Effectively assessing interactions between animals and habitat configuration: Multi-scale studies and measures

A central objective in many ecological studies is to describe and interpret abundance and distribution patterns of species or populations across habitats (Krebs 1978). However, observed patterns in ecological systems vary with scale of assessment (Wiens 1989). For example, in a study on the effect of environmental variables on the composition of marine benthic communities, Hewitt *et al.* (1998) showed that the importance of environmental conditions differed as sampling resolution changed. Scale-dependent patterns with respect to patchy habitat types have also been identified for benthic megafauna on the Grand Banks of Newfoundland (Schneider *et al.* 1987), reef fishes (Syms 1995), bald eagles (*Haliaeetus leucocephalus*) along the lower Hudson

River, New York (Thompson and McGarigal 2002), as well as juvenile Atlantic cod (Schneider *et al.* submitted). Historically, logistic convenience has dictated the scale at which analyses were executed (Schneider 2001). However single-scale studies are inadequate for addressing ecological questions for at least two reasons. At course resolutions, ecological relationships may go undetected due to loss of information. At fine resolutions high variability in data often conceals ecological patterns (i.e. increased noise; Hewitt *et al.* 1998).

Multi-scale approaches, such as scaling laws (power law relations of one variable to another) and fractal geometry (Mandelbrot 1967), are useful tools to describe how aspects of habitat change with scale. In contrast to Euclidean geometry, the measurement of a fractal object (an object with a fractal perimeter or surface) is dependent upon the scale at which it is measured, as increasing detail is observed at each level of magnification. In this way, fractal geometry is a quantitative method that can be used to describe the intrinsic spatial irregularity of natural objects and processes (Schmid 2000). Therefore, this approach has been successfully used to analyze the spatial patterning and physical structure of habitats in both terrestrial and aquatic environments. The ability to measure the spatial patterning and physical structure of a habitat in a landscape is required in order to quantify habitat fragmentation, and consequently the influences on resident organisms.

By definition, fractals are objects whose dimension is not an integer, exceed their topographical dimension (Mandelbrot 1967), and therefore cannot be adequately described by Euclidean geometry. Strict mathematical fractals are self-similar across all

scales of measurement. By contrast, fractals in nature are not infinitely self-similar, but rather demonstrate statistical self-similarity over a limited range of scales, because the objects themselves are restricted to particular scales. Fractal dimensions can be estimated from the slope of a log-log power law plot of some measurable variable against the scale at which it is measured (Kenkel and Walker 1996). Typically, the measured variable of a habitat is perimeter, and the fractal dimension provides an estimate of perimeter convolution. However, other aspects of habitat, such as area fragmentation, can also be described using fractal techniques. Because fractal analysis integrates information from multiple resolutions and effectively provides a quantitative estimate of habitat spatial patterning and fragmentation, it is a valuable method when investigating species' responses to habitat configuration.

1.5 Juvenile fish in eelgrass habitat

1.5.1 Cod collapse

For centuries, Atlantic cod were a dominant cold-water species along the continental shelves of the North Atlantic, and at its height supported an 800 thousand-tons/year fishery (Haedrich and Hamilton 2000). However, by 1992, at least 6 populations of Atlantic cod had collapsed to the point that a moratorium on fishing for this and other "groundfish" species was declared by the Canadian federal government (Hutchings and Myers 1994). This closure resulted in the loss of livelihood for nearly 30 000 Atlantic Canadians (Haedrich and Hamilton 2000) - and marked the largest lay-off of employees in Canadian labour history. In an effort to understand the collapse and

subsequent impediments to population recovery, scientists initiated a proliferation of research on the ecology and biology of Atlantic cod. These studies included a number that focused on the habitat-use ecology of juvenile cod in Newfoundland (e.g. Gotceitas and Brown 1993, Gotceitas *et al.* 1995, Fraser *et al.* 1996, Dalley and Anderson 1997, Gotceitas *et al.* 1997, Gregory and Anderson 1997, Ings *et al.* 1997, Coté *et al.* 1998, Grant and Brown 1998, Linehan *et al.* 2001, Methven *et al.* 2001, Laurel *et al.* 2003a,b, Laurel *et al.* 2004). One of the predominant findings of these studies was an association between juvenile fishes and nearshore habitat, particularly eelgrass.

1.5.2 Seagrass/eelgrass habitat

Seagrass communities are distributed along temperate coasts worldwide. Eelgrass (*Zostera marina*) is the most prevalent and widespread seagrass species, extending throughout both the northern Pacific and northern Atlantic oceans and into the Arctic Circle (den Hartog 1971). Eelgrass is predominantly a sub-tidal species throughout most of its range, although it may occur in the eulittoral zone (den Hartog 1971) and is found in a wide variety of habitats. These habitats include sheltered areas such as shallow, protected embayments, mud flats, estuaries, lagoons, and lower salt marshes (Dawson 1966), which provide substrates such as mud, firm sand, and gravel mixed with sand (den Hartog 1971). Eelgrass is a euryhaline angiosperm that is attached to the substrate via fibrous roots that extend from a horizontal rhizome. From each rhizomal node, a shoot containing 4-6 leaves extends vertically into the water column. Flowers, fruits, and seeds are produced on generative shoots that have special modifications for seed dispersal (den

Hartog 1971). Eelgrass reproduces both sexually and vegetatively, and although both processes are light and temperature dependent, it is thought that the latter likely plays a more dominant role in dispersal (den Hartog 1971).

Eelgrass grows in monospecific beds that can vary tremendously in their structural complexity (Robbins and Bell 1994). These arrangements vary from extensive, continuous meadows to highly fragmented patches arranged in a mosaic (Robbins and Bell 1994). Furthermore, examination of eelgrass growth reveals a hierarchical spatial structure that ranges from blades in shoot groups (millimetres), which extend along rhizomes (centimetres) that group to form patches (metres), and ultimately meadows (kilometres) (Robbins and Bell 1994). The structure and distribution of eelgrass appears to be largely determined by abiotic factors that include light availability, temperature, nutrient availability, wind-generated processes, tidal currents, storm events, and substrate geology and morphology (Phillips and Meñez 1989). However, biotic factors such as faunal grazing and anthropogenic disturbance may also affect structure by increasing fragmentation (Fonseca 1992). Despite these possible effects, in Newfoundland waters, eelgrass site arrangment has been shown to remain stable over at least a 5 year period (Sheppard 2002).

Ecologically, eelgrass beds play significant roles for many species. For example, eelgrass beds reduce water velocity and turbidity (Fonseca *et al.* 1982), minimize erosion and shore degradation via the stabilization of soft loose sediment, and enhance deposition of particulate matter (den Hartog 1971). In addition, eelgrass beds increase oxygen availability to a variety of fauna that live in close proximity to anoxic substrates (Kikuchi

1980). Furthermore, in the intertidal zone, eelgrass beds buffer fluctuations in temperature and salinity to inhabitants in the underlying waters (Kikuchi 1980). Eelgrass also acts as the basis for an important detrital food web (den Hartog 1971).

One of the most important, and most widely studied, roles of eelgrass is that its physical structure provides a variety of micro- and macrohabitats. For example, the differentiation of the plant body into leaves, stems, and rhizomes increases the diversity of microhabitats for epiphytic algae and associated fauna (Kikuchi 1980). Eelgrass also provides structural habitat to a variety of organisms in the form of spaces between horizontal and vertical plant structure which may help mitigate the effects of predation (den Hartog 1971, Orth *et al.* 1984). Orth *et al.* (1984) proposed that the increased faunal abundance and diversity observed in seagrass habitats compared to unvegetated habitats was largely a result of increased protection from predation afforded by these sites.

Studies on the ecological roles of eelgrass in Newfoundland waters are few, and have focused on their role as nursery habitats for juvenile fish species. Specifically, these studies have investigated predation risk to juvenile fish, such as cod, in eelgrass and unvegetated habitats (e.g. Linehan *et al.* 2001, Laurel *et al.* 2004).

1.5.3 Newfoundland juvenile fish community

As in locations elsewhere in the world, eelgrass habitat in coastal Newfoundland waters supports a greater abundance and diversity of juvenile fish than in geographically similar but less structured habitat. Three species that occupy eelgrass habitat during their

juvenile stages are Atlantic cod (*Gadus morhua*), Greenland cod (*G. ogac*), and white hake (*Urophycis tenuis*).

1.5.3.1 Atlantic cod

Atlantic cod, the most prevalent of these three species in Newfoundland waters, are located throughout the northern Atlantic Ocean (Scott and Scott 1988). In the western North Atlantic, their distribution extends from Greenland and southern Baffin Island southward to Cape Hatteras, North Carolina, USA (Scott and Scott 1988). Adult Atlantic cod spawn in the deep waters of the continental shelf (offshore stocks) and within inshore bays ("bay stocks") between late February and June depending on latitude, with more northern populations spawning earlier (Scott and Scott 1988). Atlantic cod spawn pelagically at depths of 110 m to 182 m, where females typically release 200 thousand to 12 million spherical, transparent, buoyant eggs (Scott and Scott 1988). Once fertilized, these eggs (1.2-1.6 mm in diameter) rise slowly to surface waters where they incubate and hatch after ~ 80 degree days (days x temperature (°C); Scott and Scott 1988). Larvae hatch at 3-6 mm and remain pelagic until about 25-50 mm at which point they settle to the bottom and adapt to a demersal lifestyle, either in coastal bays (Methven and Bajdik 1994) or on offshore banks (Lough *et al.* 1989).

In Newfoundland waters, age-0 Atlantic cod recruitment to nearshore habitats occurs in a series of pulses (Methven and Bajdik 1994) driven by coastal upwelling dynamics (Ings *et al.* in prep). Upon settlement, cod are associated with structurally complex habitats (Tupper and Boutilier 1995) such as cobble, fleshy macroalgae, or

eelgrass. It has been suggested that density patterns might be driven by indiscriminate settlement to all sites, combined with high site fidelity, followed by differential survival (Tupper and Boutilier 1995). However, age-0 Atlantic cod have been shown to actively discriminate habitat in the presence of a predator (Laurel *et al.* 2004). Furthermore, increasing evidence from laboratory and field experiments suggests that cod are able to distinguish between habitats prior to settlement and selectively recruit to preferred habitat.

In a laboratory setting, Gotceitas and Brown (1993) and Fraser *et al.* (1996) observed that juvenile cod utilized the interstitial spaces of cobble or kelp versus sand or pebble substrate in the presence of a predator. They suggested that juvenile cod are capable of assessing predator risk and adjusting their response accordingly. Similar findings were documented between barren and sponge-filled habitats (Lindholm *et al.* 1999). Furthermore, Gotceitas *et al.* (1995, 1997) reported that juvenile cod shifted their habitat use from fine mineral substrates to kelp or eelgrass, respectively, when exposed to an actively foraging predator. Use of eelgrass habitat has been shown to reduce predation risk for this species. In the field, Linehan *et al.* (2001) and Laurel *et al.* (2003a) described reduced predation rates on tethered age-0 cod prey in eelgrass habitat, in contrast to barren unvegetated habitats. Furthermore, Laurel *et al.* (2003a) showed that, when predator density had been controlled for statistically, predation risk increased for age-0 juvenile cod in fragmented seagrass environments (small patch sizes). Additionally, Laurel *et al.* (2004) demonstrated that post-settled cod move parallel to the shore, and that the pattern of dispersal from sites of release in mark-recapture

experiments did not resemble simple diffusion. These results stand in contrast to previous reports of very high site fidelity and limited ability to select favourable habitat (Tupper and Boutilier 1995, Grant and Brown 1998b), and instead supports the prospect of behaviourally-mediated habitat selection by juvenile Atlantic cod.

Despite evidence that links juvenile Atlantic cod and eelgrass habitat in Newfoundland coastal waters, the presence of eelgrass habitat does not guarantee high cod densities. For example, Gotceitas *et al.* (1997) found that cod densities were significantly higher in eelgrass versus non-eelgrass sites in only 2 out of 3 paired cases. Furthermore, Ings *et al.* (in prep) found that the association between high cod densities and eelgrass cover was inconsistent among years. Contrary to expectation, Schneider *et al.* (submitted) found that juvenile cod were decoupled from eelgrass habitat at scales of 5-20 m and were only correlated with eelgrass at scales greater than 20 m. This pattern suggests that presence/absence of eelgrass does not solely determine cod habitat selection.

1.5.3.2 Greenland cod

Despite their relative abundance in Newfoundland nearshore waters (Methven *et al.* 2001), few studies have investigated the ecology of Greenland cod, particularly the juvenile stage. Although once designated as a sub-species of Atlantic cod, Greenland cod have important differences in their distribution and life-histories. Greenland cod are found throughout the coastal and inshore waters of Alaska, eastward through the Canadian Arctic coast to Greenland, and southward from Labrador to Cape Breton, Nova

Scotia (Scott and Scott 1988). Greenland cod are more restricted to coastal regions throughout their lifetime than Atlantic cod. Spawning occurs from February to June (Scott and Scott 1988, Morin *et al.* 1991), in nearshore waters, with large females likely releasing 1-2 million demersal eggs (Scott and Scott 1998). In laboratory experiments, fertilized eggs (1.1-1.2 mm in diameter) hatched after approximately 25-35 days at ~2°C (Andersen *et al.* 1994), and recently-hatched, yolk-sac larvae reached 5.2 mm in length. Larvae are pelagic, however, following metamorphosis individuals settle to demersal habitat. In Newfoundland waters, settlement occurs in a single recruitment pulse in July/August (Laurel *et al.* 2003b). Age-0 Atlantic and Greenland cod are difficult to distinguish morphologically at small sizes (<50 mm; Methven and McGowen 1998). However, larger individuals can be differentiated on the basis of lateral line characteristics (Methven and McGowen 1998) and smaller individuals on differences in anal fin pigmentation.

In addition to similar morphologies, an *in situ* habitat manipulation study and field observations (Laurel *et al.* 2003b) showed that, like their congener, age-0 Greenland cod preferentially utilize eelgrass habitat versus barren areas in coastal waters of Newfoundland. In addition, prior to settlement from the pelagia to the demersal, Greenland cod also have the ability to differentiate habitat types (Laurel *et al.* 2003b), and once settled, will move among eelgrass sites (Laurel *et al.* 2004). These observations suggest that, like Atlantic cod, differences in densities of age-0 Greenland cod between sites may result from behavioural decisions rather than differential mortality alone.

Despite shared habitat requirements, Laurel *et al.* (2003b) and (2004) found that there were some differences between species in patterns of habitat use. These studies found that, during years of high conspecific density, juvenile Greenland cod were less likely to utilize sub-optimal barren habitat than Atlantic cod. They suggested that the requirement for alternative habitat-use strategies might be weaker in Greenland cod than Atlantic cod as a result of differences between life-history strategies. Specifically, they noted that because Greenland cod is an inshore spawner with demersal eggs (Scott and Scott 1989), inter-annual variability of recruitment to inshore areas is reduced because its eggs and larvae are not subject to the intense hydrographic forces as seen in the pelagic, pre-settlement stages of Atlantic cod (Bradbury *et al.* 2003). Therefore, greater inter-annual variability in recruitment by Atlantic cod may result in an increased ability to use sub-optimal habitat in high-recruitment years. Reduced use of barren substrate by Greenland cod might also be interpreted as greater dependence on eelgrass habitat. Evidence for this increased dependence was found by Laurel *et al.* (2003b) who demonstrated that Greenland cod densities decreased more than Atlantic cod densities when eelgrass was removed. A greater dependence on eelgrass habitat suggests that juvenile Greenland cod, more so than Atlantic cod, might be negatively affected by activities that compromise eelgrass habitat, such as fragmentation.

1.5.3.3 White hake

In the past decade, the abundance of juvenile white hake in coastal waters of Newfoundland (Newman Sound, Bonavista Bay) has increased steadily (Laurel *et al.*

submitted). As adults, white hake are distributed along continental slopes throughout the western North Atlantic. In North America, they are found along southern Labrador, southward to the Grand Bank, the Gulf of St. Lawrence, the Gulf of Maine, and occasionally as far south as Florida (Scott and Scott 1988, Chang *et al.* 1999). The spawning period of white hake is population-dependent; northern populations spawn in August-September, and more southerly populations (George's Bank and Middle Atlantic Bight) spawn in April and May (Chang *et al.* 1999). Female white hake, which are larger and longer-lived than males, are sexually mature at a median length of 35 cm (Chang *et al.* 1999). Fertilized eggs are 0.7-0.8 mm in diameter, contain an oil globule, and are transparent, buoyant, and pelagic (Scott and Scott 1988). Within the documented range of spawning temperatures (4-25 °C), larvae hatch from their eggs within 3-7 days, at a total length of 2 mm (Chang *et al.* 1999). Larvae remain pelagic for approximately 2 months following hatch, at which point (> 50 mm) they descend to demersal habitat (Chang *et al.* 1999). In Newfoundland waters, this transition occurs in mid- to late July.

Populations of demersal juvenile white hake (> 50 mm) are known to occupy nearshore areas along the northeastern seaboard of the United States, throughout the maritime provinces of Canada, and Newfoundland. Seagrass beds, including eelgrass, have been identified as important nursery habitat for age-0 white hake in these regions (Heck *et al.* 1989, Lazzari *et al.* 2003, Laurel *et al.* submitted). However, individuals have also been observed over muddy or sandy bottoms, in some cases burrowing into the sediment in water as shallow as 1 m deep (Scott and Scott 1988; personal observation).

Compared to the other gadids in coastal Newfoundland waters, white hake is comparatively fast-growing (35 mm/month; Chang *et al.* 1999). High growth rates combined with a relatively large gape enable white hake to switch to large demersal prey earlier than either cod species. Age-0 juvenile white hake consume polychaetes, shrimp, other crustaceans (Bowman 1981), and are even piscivorous (personal observation). These larger prey items may be more closely associated with barren substrates, and therefore high densities of white hake at highly patchy and fragmented sites may be expected. As a competitor and possible predator of sympatric young gadids, the influence of eelgrass site arrangement on age-0 white hake density may have important implication on habitat-use patterns of these other species.

1.5.4 Exploring eelgrass site heterogeneity

To examine the influence of structural arrangement rather than amount of habitat, Wells (2002) found the spatial heterogeneity (complexity) of a number of eelgrass areas in Bonavista Bay, Newfoundland and Labrador, Canada, using a fractal analysis adapted from Lovejoy (1982). At each site, Wells (2002) estimated the amount of eelgrass perimeter and area at multiple resolutions and then demonstrated how eelgrass area scales with perimeter at these sites. Wells (2002) used the scaling exponents of these relationships, $\beta_{A=f(P)}$, as an estimate of eelgrass site spatial complexity, which she then related to the density of age-0 Atlantic cod at those sites. She demonstrated a parabolic relationship between cod density and eelgrass complexity, with an intermediate

maximum. Using this technique, Hammond (2003) demonstrated the same relationship using data collected from a larger spatial scale.

Wells hypothesized that this intermediate maximum resulted from an "optimum" trade-off between food availability and predation risk when cod selected habitat (intermediate optimum hypothesis – IOH). She suggested that whereas areas with low complexity (e.g. dense meadows) provide high degrees of shelter from predators, they have too little edge, reducing physical access to prey items. Conversely, highly fragmented areas with high complexity likely have "too much edge", leading to increased risk of predation.

Although Wells' complexity index is derived from a multi-scale analysis, its behaviour with respect to changes in its components (perimeter and area) is not clear. In this thesis, I use two surveys of different geographical extent to investigate multi-scale habitat measurements that describe the association between age-0 Atlantic cod and eelgrass. In addition, I determine if single habitat characteristics - perimeter and area - drive the relationship between cod and eelgrass, or if a combined effect is important. Furthermore, I examine whether or not the same relationship between Atlantic cod and eelgrass habitat extends to the sympatric species, Greenland cod and white hake. Wells (2002) suggested, but did not test, a mechanism for the pattern of habitat use by cod that she observed. Therefore, I also explore the principle that the distribution of juvenile fish is driven by a habitat-mediated trade-off in foraging efficiency and predation risk.

1.6 References

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Co-authorship Statement

Chapter 2: Eelgrass (*Zostera marina*) patch complexity dictates age-0 fish density

This manuscript's central ideas and concepts, as well as the experimental design, were identified and developed by Maria E. Thistle, Robert S. Gregory, David C. Schneider, and Nadine Wells. Maria E. Thistle, Robert S. Gregory, and Nadine Wells aided in the collection of data. Maria E. Thistle, David C. Schneider, Danny W. Ings, and Nadine Wells contributed to the analysis and interpretation of data. Maria E. Thistle prepared this manuscript. Maria E. Thistle, David C. Schneider, and Robert S. Gregory contributed to editing this manuscript.

Chapter 3: Eelgrass (*Zostera marina*) fragmentation predicts foraging success of age-0 Greenland cod (*Gadus ogac*)

Maria E. Thistle, David C. Schneider, and Robert S. Gregory identified and developed this manuscript's central ideas and concepts. Data collection was performed by Maria E. Thistle and Robert S. Gregory. Maria E. Thistle, David C. Schneider, and Danny W. Ings contributed to the analysis and interpretation of data. Maria E. Thistle prepared this manuscript. Maria E. Thistle, David C. Schneider, and Robert S. Gregory contributed to editing this manuscript.

Chapter 2: Eelgrass (*Zostera marina*) patch complexity dictates age-0 fish density

2.1 Introduction

Over-exploitation has decimated marine ecological communities worldwide (Pauly *et al.* 1998, Tegner and Dayton 1999, Hutchings 2000, Kaiser *et al.* 2000, Myers and Worm 2003). Atlantic cod (*Gadus morhua*) populations collapsed in 1992 (Hutchings and Myers 1994) and have not recovered despite a moratorium on fishing. Recovery of a population from a collapse requires increased recruitment, and recruitment depends upon year-class strength (Swain and Sinclair 2000). The well-accepted paradigm that year-class strength depends on a critical period in marine larval life-history (Hjort 1914) was documented for Atlantic cod in the 1960s (Ings *et al.* 1997). However, since the collapse, no recruitment signal has been detected (Schneider *et al.* 1997a), indicating an additional mortality-sensitive period in cod life-history. Habitat mediated mortality has been shown for Atlantic cod and their congener, Greenland cod (*G. ogac*) (Linehan *et al.* 2001, Laurel *et al.* 2003a, Gorman 2004) during the period when juveniles occupy nearshore coastal environments (age 0-1), suggesting that appropriate habitat may afford increased survival compared to sub-optimal habitats nearby. In Newfoundland, studies have shown that post-settled juvenile cod utilize eelgrass (*Zostera marina*) beds (e.g. Gotceitas *et al.* 1997, Linehan *et al.* 2001, Laurel *et al.* 2003b), an important nursery habitat susceptible to human disturbance (Fonseca 1992). However, associations between cod and eelgrass are conditional, as cod densities measured at eelgrass versus

non-eelgrass sites are only significantly higher in every 2 out of 3 paired comparisons (Gotceitas *et al.* 1997). One explanation for this indeterminate relationship is the scale of assessment.

The relationship between the distribution or abundance of aquatic organisms and habitat has been studied extensively, but often omits the notion of scale (Adams 1976a, Adams 1976b, Orth and Heck 1980, Orth *et al.* 1984, Gibson 1994, Miranda and Pugh 1997, Ross *et al.* 1997). In addition, the metrics used to assess habitat in these studies are computed without considering scale. Historically, scale of analysis was often selected based on logistic convenience (Schneider 2001), yet spatial patterns of habitat found at small scales may be very different from those found at broader scales (Wiens 1989). Studies identifying a scale-dependent influence of habitat on organisms have become more prevalent in the past 20 years (Bell and Westoby 1986, Schneider and Piatt 1986, Farmer and Adams 1991, Syms 1995, Schneider *et al.* 1997b, Connell and Kingsford 1998, Hewitt *et al.* 1998). Specifically, scaling exponents known as fractals have been used to quantify habitat heterogeneity and shape (Gee and Warwick 1994, Davenport *et al.* 1996, Azovskii and Chertoprud 1997, Beck 1998, Palacín *et al.* 1998, Turner *et al.* 1999, O 2001, Salita *et al.* 2003) in order to examine relationships with organism distribution or abundance.

Eelgrass, the most widespread seagrass species, extends throughout the northern coastal zones of both the Atlantic and Pacific oceans (den Hartog 1971) where it grows in complex structural arrangements, from highly fragmented patches to extensive continuous monospecific meadows (Robbins and Bell 1994). While the importance of

seagrass habitat to associated fauna has been extensively investigated, the measured components rarely incorporate scale. Metrics used to assess seagrass complexity include patch size (Irlandi 1997), number of patches (Salita *et al.* 2003), shoot density (Bell and Westoby 1986 a, b, Graham et al. 1998), biomass (Adams 1976a), percent cover (Heck and Orth 1980, Salita *et al.* 2003), and leaf height (Bell and Westoby 1986a, b). Furthermore, the co-occurrence of vegetated and non-vegetated substrate has long been considered an important factor influencing many aquatic faunal species (e.g. Heck and Orth 1980, Orth *et al.* 1984, Irlandi *et al.* 1995, Barberá-Cebrián *et al.* 2002, Hyndes *et al.* 2003). However, quantification of habitat heterogeneity based on spatial patterning is rare. Examination of eelgrass growth reveals a hierarchical arrangement of spatial structure, ranging from millimetres to kilometres: from blades in shoot groups, to shoot groups in patches, to patches in meadows (Robbins and Bell 1994). Given the structure and pattern of eelgrass growth, and the potential biological importance of barren and vegetated areas, the use of fractal geometry to describe eelgrass site shape complexity is biologically appropriate (Davidson 1998, Gustafson 1998, Bogaert 2003). Using this logic, complexity, as determined by fractal analysis, refers to the spatial arrangement of eelgrass within a site, and not its abundance or density.

Wells (2002) determined the spatial heterogeneity (complexity) of different eelgrass areas in Bonavista Bay, Newfoundland and Labrador, Canada, by employing a fractal analysis adapted from Lovejoy (1982). Wells (2002) demonstrated how area scales with perimeter in eelgrass sites and derived an estimate of spatial complexity (the scaling exponent, $\beta_{A=f(P)}$), which she then related to the density of age-0 Atlantic cod at

those sites. She demonstrated a parabolic relationship between cod density and eelgrass complexity, with an intermediate maximum. Wells hypothesized that this intermediate optimum resulted from a trade-off between food availability and predation risk when cod selected habitat (intermediate optimum hypothesis – IOH). While Wells' complexity index incorporates a multi-scale approach, its behaviour with respect to changes in its components (perimeter and area) is not clear.

In this study, I re-address the findings of Wells (2002) and investigate which spatial characteristics of eelgrass sites account for the variation in age-0 Atlantic cod catch density at sites along the northeast coast of the island of Newfoundland. Specifically, I ask the following questions:

1) Do single-scale measurements of eelgrass perimeter or area explain cod distribution?

2) Do multi-scalar (fractal) measures of either perimeter or area of eelgrass explain cod distribution?

3) Does a multi-scalar (fractal) measure that combines the effects of perimeter and area of eelgrass explain cod distribution?

To assess these relationships and their consistency across different geographical ranges, I use data from two surveys (Newman Sound survey and the Fleming survey) that encompass different spatial scales. I also examine the ability to extrapolate my findings – from a species specific relationship to one including multiple guild members - by extending the investigation to two sympatric species of Atlantic cod, Greenland cod and

white hake (*Urophycis tenuis*), which potentially occupy similar niches in the nearshore community.

Based on the trade-off of Wells' (2002) intermediate optimum hypothesis, I expect that both eelgrass perimeter and area will influence fish distribution. Specifically, I expect that eelgrass structure, as determined by combined perimeter convolution and area patchiness, will describe juvenile fish densities in a parabolic fashion, with sites of intermediate complexity demonstrating highest fish densities.

2.2 Methods

2.2.1 Study areas

Data from two coastal surveys, encompassing different geographical scales, were used in this study. The Newman Sound survey extends over ~ 25 km of coastline and lies within the range of the larger Fleming survey which spans ~ 600 km of coastline, both along the eastern shore of the island of Newfoundland, Canada.

Newman Sound is a fjord that lies adjacent to Terra Nova National Park, within southwestern Bonavista Bay, Newfoundland and Labrador, Canada (Figure 2.1). An unexposed inlet, it extends 41 km in length and 1.5-3.0 km in width, and is divided into two basins by a sill located ~ 7 km from the head of the sound. Average tidal amplitude is low (1-1.5 m). The substrate and associated vegetative cover in the nearshore environment (0-15 m depth) is varied. Eelgrass is the dominant vegetation, occurring in mud, sand, and gravel substrates, and restricted to depths less than 6 m. Eight sites were

selected based on the presence of eelgrass, and the existence of concurrent juvenile Atlantic cod data.

The larger scale Fleming survey study area extends from Notre Dame Bay, southeast along Newfoundland's northeast coast to Conception Bay (Figure 2.1), encompassing the range of the Newman Sound survey. Substrate and vegetative cover found at sampling sites along this coast are similar to that in Newman Sound. Fourteen sites were identified using the same selection criteria as for the 8 sites in Newman Sound.

2.2.2 Aerial photography

Aerial photographs of the 8 Newman Sound sites, and 14 Fleming survey sites were taken in August 2000 and July 2001, respectively, in order to assess eelgrass spatial structural characteristics. Photographs were taken from a single-engine Cessna (Newman Sound survey) or deHavillard Beaver (Fleming survey) floatplane at altitudes between 250-300 m. Photographs were taken during monthly low-tide periods to allow greater visibility of substrate and vegetative cover. Flights were executed as near to midday as possible, when surface glare and winds were minimal and the sun was at its maximum height above the horizon. Images were taken with a 35 mm Pentax FX10 camera furnished with a 28-80 mm Pentax-F 200N zoom lens (set at 50 mm), and both haze and polarizing filters to reduce water surface glare.

Prior to aerial photography in Newman Sound, three fluorescent orange plywood markers (0.6 m x 0.6 m) were placed at all 8 sites to indicate the seining area, to permit calculation of the area covered by the image, and to correct for the camera angle. Two

markers were fastened to the shore at the high tide mark 25 m apart. The third marker was secured 50 m offshore by a length of rope tied to a concrete block. Floating at the water's surface, the offshore marker was placed such that it formed a right angle triangle with the onshore markers (Figure 2.2). At all 14 Fleming survey sites, the seining area and landmarks for editing images were identified using physical site characteristics, determined during ground truthing.

Aerial photographs were developed to Kodak Digital Science™ Photo CD master discs with a highest resolution of 2048 x 3072 pixels. Photos were edited and adjusted in Adobe Photoshop 5.5 by N. Wells (Newman Sound photographs) and B. Hammond (Fleming survey photographs). For a detailed description of photo manipulation techniques, see Wells (2002) and Hammond (2003).

2.2.3 Estimating eelgrass characteristics by box counting

A box counting technique (Sugihara and May 1990) was employed to quantify spatial characteristics of eelgrass (area and perimeter) at several resolutions from the aerial photographs. A grid containing 3600 boxes (1 box = 1 m^2) was positioned over each digital photograph. From this, Wells (2002) and Hammond (2003) drew by hand two hard copy replicas of each image on grids of the same dimension. On these copies, the presence/absence of eelgrass area (area measurement), and the presence/absence of eelgrass perimeter (perimeter measurement) were recorded. Grids of lower resolution (i.e. fewer boxes) were placed over the hard copy replicas, and the number of boxes containing area and perimeter were counted for resolutions of (1 m^2) 4 m^2, 9 m^2, 16 m^2,

25 m^2, 36 m^2, 100 m^2, 225 m^2, 400 m^2, and 900 m^2. Eelgrass perimeter was estimated at each resolution by multiplying the number of boxes containing eelgrass perimeter with the length (m) of the side of the box. Eelgrass area was estimated at each resolution by multiplying the number of boxes containing eelgrass area by the area (m^2) of the box (Table 2.1).

2.2.4 Multi-scale measures of structural complexity

In addition to evaluating eelgrass characteristics at single scales, I used perimeter and area estimates of eelgrass to produce multi-scale measures of spatial complexity for the 8 Newman Sound and 14 Fleming survey sites. Two of these measures were the fractal dimensions of perimeter (D_P) and area (D_A), which describe eelgrass perimeter convolution, and area patchiness, respectively (Table 2.1). D_P was calculated from the slope (scaling co-efficient) of the log-log regression of eelgrass perimeter and box length (resolution). D_A was determined in a similar fashion from the log-log regression of eelgrass area and box area (resolution). As a third measure of spatial complexity, I calculated the scaling coefficient ($\beta_{P/A}$), from a log-log plot describing how perimeter:area (using the perimeter and area estimates calculated at each scale) changes with scale of measurement (Table 2.1). It should be noted that $B_{P/A}$ was not regressed against one of its components and so the problem of part-whole correlation (Packard and Boardman 1988, Jackson et al. 1990) is not present. In the absence of part-whole correlation, the use of a ratio is a legitimate and well recognized technique for reducing the residual or error variance (Cochran 1977). As the coefficient is a negative number, I

have reported absolute values. To further understand the behaviour of this measure, I investigated how it relates to, and can be derived from, known values of D_P and D_A.

Estimated quantities of a landscape feature (e.g. perimeter or area) that remain unchanged at multiple resolutions indicate that landscapes are not truly fractal (i.e. self-similar across all scales (Mandelbrot 1983)) and only display fractal properties across a limited range of resolutions (Johnson *et al.* 1995). Of the 10 resolutions utilized, the scales over which eelgrass feature estimates changed (scaling region) were determined for each site (Kenkel and Walker 1996). This scaling region defined the resolutions over which the regression was executed. The maximum resolution used to define the scaling region was the smallest resolution giving the repeated estimate of eelgrass area (i.e. in all cases the repeated estimate for eelgrass area was 3600 m^2). This scaling region was used for the computation of all three multi-scale complexity measures.

2.2.5 Measuring juvenile fish densities

Age-0 juvenile fish densities at all Newman Sound and Fleming survey sites were estimated via a 25 m demersal beach seine. The seine was deployed 55 m from shore from a 6 m boat, and was retrieved by two individuals on shore standing 16 m apart. Pulled along the seafloor, the seine samples the bottom 2 m of the water column, covering approximately 880 m^2 of demersal habitat. Deployed in this manner, SCUBA observations have demonstrated that the seine catches 95% of the fish fauna in its path (Gotceitas *et al.* 1997) and induces negligible mortality. A detailed description of the seine's construction, deployment, and retrieval is located in Schneider *et al.* (1997c).

Collected fish were transferred to containers of seawater, counted, measured, and identified to species. Fish were measured to standard length (most anterior point to caudal peduncle) then aged by applying previously established age-length relationships for these species (Gregory *et al.* 2000). Fish were released to their site of capture following sorting.

Fish density data were collected from the 8 Newman Sound sites on a bi-weekly basis for the month of September from 1998-2002. Data from September were analyzed for comparability with previous studies investigating eelgrass structure and fish densities in Newman Sound (Wells 2002). Fish density data collected during 1999 and 2000 at two sites - Buckley's Cove (BC) and Dockside (DS) – were not included due to a concurrent habitat manipulation experiment (Laurel *et al.* 2003b). Fish density data from 14 Fleming survey sites were collected September - October of 1996, 1997, and 2001. Atlantic cod density data were available for both the Newman Sound and Fleming surveys, however Greenland cod and white hake data were only available from the Newman Sound survey.

2.2.6 Relating juvenile fish density to habitat structural complexity

In keeping with Wells (2002), I investigated the relationships between age-0 juvenile Atlantic cod density and the eelgrass complexity indices D_P, D_A, and $\beta_{P/A}$, utilizing all densities greater than zero for both the Newman Sound and Fleming surveys. I also investigated the relationships between the densities of each of two co-occurring species, age-0 Greenland cod (*Gadus ogac*) and age-0 white hake (*Urophycis tenuis*), and

$\beta_{P/A}$ in the Newman Sound survey. Densities were computed as number of fish/seine haul (number of fish/ 880 m^2). I analyzed both surveys separately, as sampling intensity was greater in the Newman Sound survey than the Fleming survey (3 sampling dates per year for 5 years in Newman Sound sites versus one sampling date per year for 3 years at Fleming sites). Analyses were completed for each species by regressing fish density for all years against each complexity index in a quadratic model.

I performed all analyses using a log link and a normal error distribution (McCullagh and Nelder 1987), and I examined residuals for the assumptions of homogeneity, independence, and normality. If a normal error distribution was inappropriate, a gamma error structure was used. Analyses were executed using the Gen mod procedure in SAS (1988). The tolerance of type I error was $\alpha = 0.05$.

2.3 Results

2.3.1 Density of age-0 Atlantic cod vs. single-scale measures of eelgrass structure

The relationships between age-0 Atlantic cod densities and both eelgrass perimeter and eelgrass area differed depending on the scale of measurement (Figure 2.3). For example, fish density appeared to increase with perimeter and area at 400 m^2 resolution, but at 1 m^2 resolution appeared to be parabolic with an intermediate optimum or showed no pattern with respect to perimeter and area, respectively. In addition, information was lost as resolutions became coarser, influencing pattern interpretation.

That is, the apparent change in patterns results from condensation of information as resolution – box size – increases.

2.3.2 Multi-scale analysis of eelgrass habitat structure

Log-log plots of perimeter, area, and perimeter:area versus scale of measurement produced a D_P, D_A, and $\beta_{P/A}$, respectively, for each of the 8 Newman Sound and 14 Fleming survey sites (e.g. plots for Mistaken Cove (MI) in Figure 2.4). Values of D_P can range from $1 < D_P < 2$ (Mandelbrot 1983, Barnsley 1988), with increasing values representing sites that have increasingly convoluted eelgrass/non-eelgrass boundaries. Values of D_P ranged from 1.0721 to 1.6731 in the Newman Sound survey and from 1.1602 to 1.7306 in the Fleming survey (Table 2.2). Values of D_A can range from $0 < D_A < 1$ (Mandelbrot 1983, Barnsley 1988). Values approaching 0 represent sites with an increasingly sparse, discontinuous eelgrass arrangement. Values approaching 1 represent sites that are increasingly uniform and continuous, while intermediate values represent sites that are patchy or fragmented. Values of D_A ranged from 0.8816 to 0.9737 in the Newman Sound survey and from 0.7359 to 0.9408 in the Fleming survey (Table 2.2). While sites in the Fleming survey spanned a broader range of values of D_A, ranges in both surveys suggest sites with limited fragmentation and patchiness.

Absolute values of $\beta_{P/A}$ ranged from 0.2216 to 0.8730 in the Newman Sound survey, and from 0.3713 to 0.8489 in the Fleming survey (Table 2.2). Larger values of $|\beta_{P/A}|$ represent sites whose estimate of perimeter:area changes greatly with scale, and therefore demonstrate eelgrass arrangements of greater complexity. To confirm that

increasing values of $|\beta_{P/A}|$ represented sites with increasing perimeter convolution and area fragmentation, I established that the parameter can be derived from estimates of D_P and D_A in the following manner:

Since:

$$\frac{P:A}{P_o:A_o}=\left(\frac{L}{L_o}\right)^{\beta_{P/A}} \tag{2.1}$$

then,

$$\left(\frac{P}{A}\right)\left(\frac{A_o}{P_o}\right)=\left(\frac{L}{L_o}\right)^{\beta_{P/A}} \tag{2.2}$$

and,

$$\left(\frac{P}{P_o}\right)\left(\frac{A_o}{A}\right)=\left(\frac{L}{L_o}\right)^{\beta_{P/A}} \tag{2.3}$$

Substituting for P/P_o (Table 2.1) and reciprocating A_o/A,

$$\left(\frac{L}{L_o}\right)^{1-D_P}\left(\frac{A}{A_o}\right)^{-1}=\left(\frac{L}{L_o}\right)^{\beta_{P/A}} \tag{2.4}$$

Now substituting for A/A_o (Table 2.1) gives,

$$\left(\frac{L}{L_o}\right)^{1-D_P}\left[\left(\frac{L}{L_o}\right)^{2-2D_A}\right]^{-1}=\left(\frac{L}{L_o}\right)^{\beta_{P/A}} \tag{2.5}$$

Therefore, as the bases of each term are the same, solving for $\beta_{P/A}$ shows,

$$(1-D_P)+(-2+2D_A)=\beta_{P/A} \tag{2.6}$$

and,

$$2D_A-D_P-1=\beta_{P/A} \tag{2.7}$$

Using a derivation of Wells' (2002) fractal measure, $\beta_{A=f(P)}$ (Appendix A), I compared $\beta_{P/A}$ to $\beta_{A=f(P)}$ across various values of D_P and D_A. I plotted each scaling coefficient against values of D_P and D_A (Figure 2.5). This comparison revealed that while $\beta_{P/A}$ changed monotonically with respect to D_P and D_A, $\beta_{A=f(P)}$ exhibited a behaviour which may result in a single value representing sites of very different structural complexity (Figure 2.6).

2.3.3 Density of age-0 fish vs. multi-scale measures of eelgrass structural complexity

For both surveys, age-0 Atlantic cod data were combined for all years and compared to each of the three multi-scale structural complexity measures, D_P, D_A, and $|\beta_{P/A}|$, in the following model:

$$D = e^{\mu} + \varepsilon \tag{2.8a}$$

$$\mu = \beta_o + \beta_C \cdot C + \beta_{C^2} \cdot C^2 + \beta_Y \cdot Y + \beta_{Y \cdot C} \cdot Y \cdot C + \beta_{Y \cdot C^2} \cdot Y \cdot C^2 \tag{2.8b}$$

where D = cod density (#/seine haul), C = complexity index (D_P, D_A, or $|\beta_{P/A}|$), and Y = year. Normal error distributions were not appropriate for any analysis, and gamma distributions were employed instead. Neither of the interaction terms, $\beta_{Y \cdot C} \cdot Y \cdot C$ and $\beta_{Y \cdot C^2} \cdot Y \cdot C^2$, nor the year term, $\beta_Y \cdot Y$ were significant for each of the 3 analyses in the Newman Sound survey, and therefore were removed from further analysis (Table 2.3). The same was true of the analyses for D_A and $|\beta_{P/A}|$ in the Fleming survey (Table 2.3). In these cases, I used a gamma distribution and tested the model:

$$D = e^{\mu} + \varepsilon \tag{2.9a}$$

$$\mu = \beta_o + \beta_C \cdot C + \beta_{C^2} \cdot C^2 \qquad (2.9b)$$

Significant $\beta_{Y \cdot C} \cdot Y \cdot C$ and $\beta_{Y \cdot C^2} \cdot Y \cdot C^2$ interactions existed for the Fleming survey data when the complexity measure was D_P.

The relationship between cod density and eelgrass perimeter convolution (D_P) was inconsistent between surveys, and therefore across geographical scales. The relation of cod density to D_P in the Newman Sound survey demonstrated a significant negative (downward opening) quadratic ($\beta_{(D_P)}$: $X^2 = 16.84$, $p < 0.0001$, $\beta_{(D_P^2)}$: $X^2 = 16.36$, $p < 0.0001$, Table 2.4, Figure 2.7). In the larger scale Fleming survey, the cod density-D_P relationship significance depended on year. In 2001, the significant relationship produced a positive (upward opening) quadratic ($\beta_{(D_P)}$: $X^2 = 9.33$, $p = 0.0023$, $\beta_{(D_P^2)}$: $X^2 = 8.67$, $p = 0.0032$, Table 2.4), however no significant quadratic or linear relationship was present in 1996 ($\beta_{(D_P)}$: $X^2 = 3.03$, $p = 0.0815$ and $\beta_{(D_P^2)}$: $X^2 = 3.53$, $p = 0.0602$, respectively) or 1997 ($\beta_{(D_P)}$: $X^2 = 2.04$, $p = 0.1530$ and $\beta_{(D_P^2)}$: $X^2 = 2.27$, $p = 0.1317$, respectively).

I found a similar inconsistency between surveys (geographical scales) in the relationship between cod density and patchiness/fragmentation of eelgrass area. I observed a significant negative quadratic relationship between cod density and D_A in the Newman Sound survey ($\beta_{(D_A)}$: $X^2 = 5.43$, $p = 0.0197$, $\beta_{(D_A^2)}$: $X^2 = 5.41$, $p = 0.0201$, Table 2.4, Figure 2.7) while data from the Fleming survey unveiled a significant positive quadratic ($\beta_{(D_A)}$: $X^2 = 15.77$, $p < 0.0001$, $\beta_{(D_A^2)}$: $X^2 = 15.30$, $p < 0.0001$, Table 2.4, Figure 2.7).

Consistent, significant, negative quadratic relationships were found between cod-density and $|\beta_{P/A}|$ for both surveys (Newman Sound survey: $\beta_{(|\beta P/A|)}$: $X^2 = 9.81$, $p = 0.0017$, $\beta_{(|\beta P/A|^2)}$: $X^2 = 9.02$, $p = 0.0027$. Fleming survey: $\beta_{(|\beta P/A|)}$: $X^2 = 7.75$, $p = 0.0054$, $\beta_{(|\beta P/A|^2)}$: $X^2 = 7.67$, $p = 0.0056$. Table 2.4, Figure 2.8). These relationships demonstrate an intermediate maximum of age-0 Atlantic cod density with respect to habitat complexity at two spatial scales of sampling.

Relating cod density to $|\beta_{P/A}|$ yielded similar statistically significant patterns in both datasets representing different geographical scales. Therefore, I investigated the relationship between $|\beta_{P/A}|$ and age-0 densities of two sympatric species, Greenland cod (*Gadus ogac*) and white hake (*Urophycis tenuis*) using Newman Sound survey data. I used the same model to evaluate the Greenland cod density-$|\beta_{P/A}|$ relationship as was used to assess the Atlantic cod density-$|\beta_{P/A}|$ relationship (equation 2.8). As in the previous analyses, a normal error distribution was not appropriate and a suitable gamma distribution was employed instead. Again, neither of the interaction terms, $\beta_{Y \cdot C} \cdot Y \cdot C$ and $\beta_{Y \cdot C^2} \cdot Y \cdot C^2$, nor the year term, $\beta_{Y} \cdot Y$ were significant (Table 2.3), and so the reduced model with a gamma distribution (equation 2.9) was used to test for significance. Similar to the Atlantic cod data, the Greenland cod density-$|\beta_{P/A}|$ relationship produced a significant, negative quadratic ($\beta_{(\beta P/A)}$: $X^2 = 10.73$, $p = 0.0011$, $\beta_{(\beta P/A^2)}$: $X^2 = 13.71$, $p = 0.0002$. Table 2.4, Figure 2.8).

The extended model (equation 2.8) with a normal error distribution was applied to the white hake density-$|\beta_{P/A}|$ relationship, however the assumptions were not met and a

gamma distribution was used instead. Neither of the interaction terms, $\beta_{Y\cdot C}\cdot Y\cdot C$ and $\beta_{Y\cdot C^2}\cdot Y\cdot C^2$, nor the year term, $\beta_Y\cdot Y$ were significant (Table 2.3), and so the truncated model (equation 2.9) using a normal distribution was applied instead. Using this model, and like Atlantic cod and Greenland cod, the white hake density-$|\beta_{P/A}|$ relationship yielded a significant, negative, parabolic result ($\beta_{(|\beta P/A|)}$: $X^2 = 11.01$, $p = 0.0009$, $\beta_{(|\beta P/A|^2)}$: $X^2 = 12.28$, $p = 0.0005$. Table 2.4, Figure 2.8).

White hake settled in Newman Sound prior to either cod species in the years of this study. Consequently, they were larger than cod by September, and hence, may not be comparable with respect to habitat use. To account for this possibility, I tested whether or not the white hake density-$|\beta_{P/A}|$ relationship demonstrated the same pattern in August (when white hake would be a comparable size to cod in September) using the model:

$$D = e^{\mu} + \varepsilon \tag{2.10a}$$

$$\mu = \beta_o + \beta_C \cdot C + \beta_{C^2} \cdot C^2 + \beta_M \cdot M + \beta_{M\cdot C} \cdot M \cdot C + \beta_{M\cdot C^2} \cdot M \cdot C^2 \tag{2.10b}$$

where C = complexity index (in this case, $|\beta_{P/A}|$) and M = month (August or September). The model was executed with a normal error distribution. The patterns in August and September differed significantly ($\beta_{M\cdot C^2}$: $X^2 = 9.38$, $p = 0.0022$), and (using equation 2.9) there was no significant linear or quadratic relationship between white hake density and $|\beta_{P/A}|$ in August ($\beta_{(|\beta P/A|)}$: $X^2 = 0.28$, $p = 0.5963$, $\beta_{(|\beta P/A|^2)}$: $X^2 = 1.68$, $p = 0.1952$).

2.4 Discussion

This study demonstrates that the density distribution of age-0 Atlantic cod in Newfoundland waters is explained by eelgrass site complexity, which includes a combined effect of eelgrass edge (perimeter) convolution and eelgrass area fragmentation ($\beta_{P/A}$). In accordance with the intermediate optimum hypothesis (IOH) (Wells 2002), the relationship is parabolic, with density of cod greatest at intermediate complexities. I have demonstrated that this relationship exists at two different geographical scales, and that the density-$\beta_{P/A}$ relationship applies to two additional sympatric species, Greenland cod and white hake during the month of September. The results of this study show that neither single-scale estimates of eelgrass perimeter or area, nor multi-scale measures of eelgrass perimeter convolution (D_P) nor eelgrass area fragmentation (D_A) are sufficient to explain juvenile Atlantic cod distribution patterns.

2.4.1 Measuring habitat configuration

Previous studies have attempted to describe the effects of habitat configuration on resident organisms using scale-specific measures. For example, single scale assessments concerning possible edge effects of seagrass landscapes typically compare 'edge' and 'interior' zones (Bologna and Heck 2002, Hovel and Lipcius 2002, Jackson *et al.* 2006) or 'categories of fragmentation' (Frost *et al.* 1999, Hovel and Lipcius 2002), examine patch size (Irlandi *et al.* 1995, Irlandi 1997, Bell *et al.* 2001, Hovel 2003, Laurel *et al.* 2003), percent cover (Hovel 2003), distance to nearest patch (Turner *et al.* 1999, Hovel

2003), shoot density (Hovel and Lipcius 2002, Hovel 2003), or ratios of individual patch perimeter and area (Salita *et al.* 2003, Jackson *et al.* 2006). Depending on the measure and species of interest, these studies have demonstrated varied influences of fragmentation on the density and survival of seagrass-associated fauna. For example, Bell *et al.* (2001) found no relationship between fish density and patch size, amphipods and patch size, or infaunal polychaetes and interior/edge habitat. Contrary to these results, Bologna and Heck (2002) reported that amphipod and polychaete densities were significantly greater at seagrass edges than interiors. In a study concerning juvenile blue crab survival and abundance, Hovel and Lipcius (2002) found that densities were greater in patch interiors than edges, and increased with shoot density, but that there was no relation to patch size. They also found that survival of crab was reduced in isolated patches, and decreased with shoot density - the latter of which was attributed to high incidents of predation by older conspecifics. Patch size, however, was found to affect tethered juvenile cod survival, as Laurel *et al.* (2003a) found that predation rates were negatively correlated with the size of artificial eelgrass patches.

While there is a strong focus in the literature on the influence of 'patchy', 'edgy', and fragmented habitat on occupant organisms, as well as a call to move from individual patch-studies to patches in landscapes (Frost *et al.* 1999, Hokit *et al.* 1999, Bell *et al.* 2001, Jackson *et al.* 2006), remarkably few studies use a multi-scale measure to obtain a quantitative estimate of fragmentation or edginess, such as D_P, D_A, or $\beta_{P/A}$. I identified only two studies that examined the effect of a fractal measure of seagrass complexity on its associated faunal community (Turner *et al.* 1999, Salita *et al.* 2003). Salita *et al.*

(2003), in an investigation concerning the effects of seagrass configuration on fish communities, reported a statistically significant, positive parabolic relation between fish abundance (% fish caught relative to control site) and a composite measure of patch configuration ("continuity of vegetation") extracted by principle component analysis of six variables. However, of the six, 'percent cover' had the largest factor weight (0.93) on the first principle component, thus making it difficult to differentiate between the effects of percent cover and configuration in their analysis. Not surprisingly, the relation of fish abundance to percent cover estimated from their data ($r^2 = 0.66$ in February and $r^2 = 0.67$ in June) approaches that for the relation of abundance to PC1 ($r^2 = 0.71$ in February and $r^2 = 0.94$ in June). A reanalysis of their data shows that the effect of configuration on fish abundance can be separated from the PCA composite measure by using multiple regression to control for percent cover. When the relation of fish abundance to percent cover is controlled by regression, there was no relation of fish abundance to the other 5 measures of patch configuration ($F_{5,4} = 0.81$, $p = 0.599$ in February, $F_{5,4} = 3.73$, $p = 0.113$ in June). Further analysis showed that there was no relation of fish density to a principle component based on 5 measures of configuration, omitting percent cover from the ordination ($F_{2,7} = 2.2$, $p = 0.181$ in February, $F_{2,7} = 3.66$, $p = 0.082$ in June). Turner *et al.* (1999) showed that a fractal measure of seagrass perimeter contributed to an overall canonical correlate of invertebrate community structure with environmental factors. However, Turner *et al.* (1999) did not directly measure the relation of faunal abundance or community structure to a fractal measure.

In other systems, studies that have used fractal analysis to describe habitat have primarily used a measure analogous to D_P and have found differing effects on the density of the associated fauna. In a study on gastropod density in rocky intertidal and mangrove habitats, Beck (1998) used fractal analysis to describe the degree of convolution of linear segments of the substrate. He determined that gastropod density increased with fractal dimension (D) on rocky intertidal shores, but showed no significant pattern with the higher values of D common to mangrove habitat. Taniguchi and Tokeshi (2004), in another experiment of substrate surface irregularity, demonstrated a season-dependent increase in the density of some freshwater invertebrate species with increasing fractal dimension of stream bottoms. At least two other studies have found no relation between resident fauna and fractal dimension of habitat: a study on spider diversity in shrub patches (Whitehouse *et al.* 2002), and barnacle larvae settlement to benthic substrates (Hills *et al.* 1999).

It has been suggested that the limited use of fractal analysis to assess habitat complexity stems from criticism that the measures used are statistical and lacking biological content (e.g. Beck 1998, Imre and Bogaert 2004). However, the scaling exponent, $\beta_{P/A}$, is more informative than estimates of perimeter convolution or area fragmentation alone in a two-component habitat system, is statistically accurate, and is biologically interpretable. D_P accurately describes the boundary between both habitat types in these systems (e.g. eelgrass and unvegetated substrate), but provides no information on which side of this boundary the eelgrass lies. Therefore, sites with the same D_P value can have dramatically different appearances and biological implications.

Therefore, fractal measurements of boundaries are most functional in habitat use studies when they describe the boundary between a usable and unusable landscape feature (e.g. the distribution of juvenile cod along coastlines of differing fractal dimension (Ings *et al. in prep*) or the distribution of gastropods along linear transects of rocky substrate with differing fractal dimension (Beck 1998, 2000)). In a mixed-habitat system, interpreting D_P can best be accomplished in concert with an area measurement of the habitat of interest. $\beta_{P/A}$ combines both of these elements in a way that is appropriate in terms of the mathematical definitions of perimeter and area, and the biological implications of perimeter:area ratios. Lovejoy (1982) used perimeter-area relationships to determine the fractal dimension of a patch's perimeter convolution using several differently sized patches, one single scale estimate of each patch's perimeter and area, and the assumption that the patches are self-similar ($P = kA^{D/2}$, where P is perimeter, A is area, k is a constant, and D is the fractal dimension of perimeter). Wells (2002) extended this method, measuring the same landscapes at different resolutions, and while this scaling coefficient ($\beta_{f(A)=P}$) can be interpreted in terms of perimeter convolution and area fragmentation (Appendix 1), it resulted from the regression of two estimated quantities. $\beta_{P/A}$ avoids the statistical problem of regression against a variable measured with error, as it quantifies a change in perimeter:area with respect to a fixed measure (resolution (m)). In addition, $\beta_{P/A}$ provides a less ambiguous estimate of habitat complexity than $\beta_{f(A)=P}$. By investigating the behaviours of both $\beta_{P/A}$ and $\beta_{f(A)=P}$ via manipulating values of their components, D_P and D_A, I have demonstrated that values of $\beta_{f(A)=P}$, in contrast to $\beta_{P/A}$,

may represent multiple sites with very different structural complexities. Hence, the use of $\beta_{f(A)=P}$ is fraught with compromises.

2.4.2 What process generates the parabolic relation of cod to eelgrass complexity?

I found a parabolic distribution with an intermediate maximum of age-0 Atlantic cod density with respect to $\beta_{P/A}$. The ability to discriminate and selectively recruit to preferred habitat (Gregory and Anderson 1997, Laurel *et al.* 2003b) suggests that the pattern observed between cod density and $\beta_{P/A,}$ might result from a trade-off in feeding and predator avoidance. Wells' Intermediate Optimum Hypothesis (2002), suggests that eelgrass sites of intermediate structural complexity might provide adequate opportunity for juvenile cod to forage on zooplankton and benthic invertebrates over sandy, unvegetated areas, while providing enough structural refuge in which to camouflage or evade predators.

Structural refuge has been shown to be important to juvenile Atlantic cod in a number of lab (cobble: Gotceitas and Brown 1993, Fraser *et al.* 1996; sponges: Lindholm *et al.* 1999) and field based studies (kelp: Gotceitas *et al.* 1995; eelgrass: Gotceitas *et al.* 1997, Linehan *et al.* 2001, Laurel *et al.* 2003a). In these investigations, cod used structure in the presence of a predator, and effectively reduced predation rates. The use of structured habitat to offset predation is well documented in the animal kingdom (reviewed by Lima and Dill 1990). Habitats with an intricate morphology have been shown to provide protection from predation to juvenile fish in a number of species, including bluegill sunfish *Lepomis macrochirus* (Crowder and Cooper 1982, Savino and

Stein 1982, Werner *et al.* 1983, Gotceitas and Colgan 1987, 1989), cunner *Tautogolabrus adspersus* (Tupper and Boutilier 1997), and red drum *Sciaenops ocellatus* (Rooker *et al.* 1998). Protection for prey results from impaired swimming and searching abilities of predators (Crowder and Cooper 1982, Savino and Stein 1982, Orth *et al.* 1984, Mattila 1992), as well as increased crypsis and anti-predatory behaviours (Savino and Stein 1982, 1989).

Studies of structural refuge characteristics and behaviours such as these, along with the previously described investigations of patchy habitats, support the interpretation that less fragmented eelgrass sites reduce predation risk to age-0 Atlantic cod. Likewise, they also provide support for reduced foraging ability under the same habitat conditions as several studies investigating the effects of physical structure on predation have been conducted between fish and their planktonic/invertebrate prey (e.g. Heck and Thorman 1981, Crowder and Cooper 1982, Matilla 1992, James and Heck 1994). Borg *et al.* (1997) suggested that juvenile cod utilize protective cover to offset predation during the day, and forage over barren areas under the cover of darkness at night. As these studies demonstrate a requirement for both open substrate and protective cover, they strengthen arguments in support of the intermediate optimum hypothesis.

The requirement for fish to have access to both vegetated and unvegetated habitat has been noted by several authors (e.g. Orth *et al.* 1984, Holt *et al.* 1983, Jackson *et al.* 2006). Mittelbach (1981) suggested that the reason why juvenile sunfish were not found in open areas where the potential for growth was highest was due to the lack of protective cover found away from the vegetated littoral zone. This requirement to forage in open

areas adjacent to protective sites is common to many species, including invertebrates such as web-building spiders (Bilde *et al.* 2002) and the American lobster (Spanier *et al.* 1998), birds such as tits (*Parus spp.* - Walther and Gosler 2001) and black-capped chickadees (Lima 1985), as well as mammalian species including grey squirrels (Lima *et al.* 1985), guinea pigs (Cassini and Galante 1992), and mule deer (Pierce *et al.* 2004).

Other possible explanations of a parabolic relation of juvenile Atlantic cod to eelgrass complexity do not entail a trade-off, but rather derive from the influence of either predators or food availability alone. In a predator-driven scenario, predation risk is elevated at highly fragmented/convoluted sites due to increased edge effects and exposure to predators. Likewise, predation is also high in continuous meadows due to high densities of predators. High predation rates at both continuous and highly fragmented sites would reduce the density of age-0 cod in these sites, relative to intermediate ones, resulting in a parabolic distribution. Laurel *et al.* (2003a) detected these two mechanisms influencing predation risk in a study of eelgrass patch size and predation of juvenile cod. They found that predation rates were negatively correlated with patch size, however in large eelgrass patches (22 m^2), predation of cod was higher than expected due to high predator densities. In a food-driven scenario, cod densities respond to densities of food resources, which could be higher at eelgrass sites of intermediate complexities (e.g. mysid assemblages: Barberá-Cebrián *et al.* 2002). Alternatively, *accessibility* might be greatest at sites of intermediate eelgrass complexity due to high densities of prey in vegetated areas (e.g. harpacticoid copepods: Jenkins *et al.* 2002).

2.4.3 Comparing patterns and interpretations for all three species

In this study, I have demonstrated that age-0 Greenland cod, like Atlantic cod, are distributed parabolically with respect to eelgrass habitat complexity ($|\beta_{P/A}|$). A larger X^2 (chi square) value for the parabolic term in the Greenland cod-eelgrass relationship than in the Atlantic cod-eelgrass relationship ($X^2 = 13.71$ vs. $X^2 = 9.02$) indicates a larger 'improvement of fit' upon addition of the quadratic term for the former species. This suggests a stronger relationship with respect to spatial complexity than Atlantic cod. Other studies on age-0 Greenland cod have suggested that this species is more dependent on eelgrass habitat than Atlantic cod. Laurel *et al.* (2003b) determined that prior to settlement from the pelagia to the demersal, Greenland cod, like their congener, have the ability to differentiate habitat types, and are capable of moving between eelgrass sites (Laurel *et al.* 2004). However, during years of high conspecific density, juvenile Greenland cod were less likely to utilize suboptimal barren habitat than their congeners (Laurel *et al.* 2004). Furthermore, in a before/after study on the effects of removing eelgrass, Greenland cod densities decreased more than Atlantic cod densities (Laurel *et al.* 2003b). The greater decrease in Greenland versus Atlantic cod densities following eelgrass removal suggests that the increased use of barren habitat by Atlantic cod observed by Laurel *et al.* (2004) was not caused by competative displacement by Greenland cod. Rather, as for Atlantic cod, the parabolic relation of Greenland cod density to $|\beta_{P/A}|$ might result from a habitat-mediated trade-off between feeding and

protection from predators. However, neither foraging strategy, nor anti-predatory behaviours have been examined in juvenile Greenland cod.

Prior to this study, patterns of juvenile hake distribution in eelgrass habitat in nearshore Newfoundland waters had not been explored. I have shown that age-0 white hake occupy eelgrass sites in Newfoundland waters, and that, like co-habitant cod species, the relation of hake density to eelgrass site complexity can be described by a negative quadratic relationship. This relation, while evident in September, was not evident in August. Despite the improved fit afforded by the addition of the quadratic term ($X^2 = 12.28$, $p = 0.0005$), Figure 2.8 shows that at high values of $|\beta_{P/A}|$, hake densities remain elevated. A balance in foraging and predator evasion may also drive this pattern of eelgrass habitat use. However, this pattern suggests that in highly convoluted and fragmented sites, increased foraging opportunities and/or decreased predation risk are available to white hake more so than cod species. There are a number of factors that might allow white hake to exploit the barren substrates afforded at sites of high $|\beta_{P/A}|$. With growth rates close to 1.0 mm/day (Lang *et al.* 1996), size-selective foraging (Coates *et al.* 1982), and a relatively large gape, age-0 hake may 'outgrow' the predator field located in these relatively shallow nearshore sites, and therefore, more easily exploit patchy eelgrass sites. Relief from predation on open substrates might also result from the more sedentary demersal lifestyle employed by white hake, as compared to the more mobile cod species. Alternatively, as a burst swimmer, white hake may demonstrate better escape behaviour than both cod species. As an ambush predator, white hake remain stationary to avoid detection by prey items. Similarly, white hake may exploit

this tactic in barren areas, evading dangerous predator encounters. Additionally, the higher thermal tolerance of white hake may allow individuals to utilize barren areas within sites with a high $|\beta_{P/A}|$ in warmer, shallow waters. In this way, juveniles may avoid predation from larger fish which are unlikely to occupy shallow waters. In addition, occupying shallow areas might allow hake to reduce competition from other gadids with lower thermal tolerances.

2.4.4 Implications and Conclusions

This investigation is one of few studies to assess a relation of populations to habitat at two different geographical scales: a bay scale (25 km coastline) and a coastal scale (600 km coastline). In this way, I have confirmed the finding that age-0 Atlantic cod densities depend on the configuration of eelgrass habitat across a sizable fraction of their range in the northwest Atlantic. The ability to extrapolate results from fine-scales to broad-scales may permit more effective management of natural resources, as well as allow investigators to understand underlying biological principles. Furthermore, this study is the first to use a fractal measure ($\beta_{P/A}$) that describes both the perimeter convolution and area fragmentation of a two-component habitat system (i.e. eelgrass and barren substrate) on a landscape scale. This methodology has advantages over traditional single scale assessments, including incorporation of multiple resolutions appropriate to the cod-eelgrass system and the ability to assess the habitat component of interest (landscape shape or arrangement) using a single measure.

The parabolic distribution of age-0 Atlantic cod with respect to eelgrass site complexity ($\beta_{P/A}$) may play an important role in understanding the mortality-sensitive period during the juvenile phase, given the evidence for habitat mediated survival during this life-stage. If the arrangement of eelgrass habitat influences the survival and success of age-0 cod, consistent with the intermediate optimum hypothesis, this knowledge can enable researchers to identify habitat that should be protected and monitored. Identifying valuable habitat, including the influence of spatial configuration of habitat on juvenile cod survival, may facilitate the recovery of the population collapse that occurred in the early 1990s.

I have demonstrated that the density of other species, Greenland cod and white hake, are also influenced by the spatial arrangement of eelgrass. It is likely that in other systems, species utilizing or affected by ecotones may be influenced by the spatial configuration of their two-component habitat system. In these cases, $\beta_{P/A}$ provides a single measure to assess the two-dimensional configuration of the system and the response in terms of species density or richness. Furthermore, if a trade-off in feeding and predator avoidance drives distribution of individuals, a parabolic relationship may apply to any species requiring open areas in which to forage as well as shelter to offset predation risk.

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Table 2.1: Parameters and variables used in multi-scale analysis of eelgrass site structural complexity

Parameters and Variables	Symbol	Definition	Mathematical definition
Length	L	The extent of one side of a box at one resolution in the box-counting technique protocol	
	L_o	The extent of one side of a box at a different resolution in the box-counting technique protocol	
Perimeter	P	The length of the boundary between eelgrass and non-eelgrass substrate for one resolution	$P = (L)(\#\, boxes\ at\ resolution\ L)$
	P_o	The length of the boundary between eelgrass and non-eelgrass substrate for a different resolution	$P_o = (L_o)(\#\, boxes\ at\ resolution\ L_o)$
Area	A	The 2-dimensional eelgrass surface included by an eelgrass/non-eelgrass boundary for one resolution	$A = (L^2)(\#\, boxes\ at\ resolution\ L)$
	A_o	The 2-dimensional eelgrass surface included by an eelgrass/non-eelgrass boundary for a different resolution	$A_o = (L_o^2)(\#\, boxes\ at\ resolution\ L_o)$
Fractal dimension of perimeter	D_P	Equal to 1 minus the scaling coefficient describing how perimeter estimates change with scale. Indicates edge convolution.	$\frac{P}{P_o} = \left(\frac{L}{L_o}\right)^{1-D_P}$
Fractal dimension of area	D_A	Equal to 1 minus the scaling coefficient describing how area estimates change with scale. Indicates area fragmentation.	$\frac{A}{A_o} = \left(\frac{L^2}{L_o^2}\right)^{1-D_A}$

Scaling coefficient of P:A vs. resolution	$\beta_{P:A}$	Scaling coefficient describing how perimeter:area estimates change with scale. Indicates convolution and patchiness.	$\frac{P:A}{P_o:A_o}=\left(\frac{L}{L_o}\right)^{\beta_{P/A}}$

Table 2.2: Values of multi-scale eelgrass structural complexity measures, and maximum scaling region resolution for 8 Newman Sound survey (NS) sites and 14 Fleming survey (FS) sites

Survey	Site	D_P	D_A	$\lvert\beta_{P/A}\rvert$	Maximum Scaling Region Resolution (m^2)
NS	BB	1.0721	0.9252	0.2216	900
	DS	1.5812	0.9701	0.6110	100
	WR	1.6270	0.9514	0.7242	225
	MI	1.5370	0.9500	0.6370	400
	BC	1.5330	0.9737	0.5856	100
	HC	1.2628	0.9383	0.3861	400
	MC	1.6731	0.9680	0.7354	225
	SB	1.6362	0.8816	0.8730	900
FS	18	1.4568	0.8591	0.7386	400
	32	1.1921	0.7597	0.6727	400
	34	1.4911	0.9482	0.5947	400
	46	1.7306	0.9408	0.8489	400
	52	1.5006	0.8624	0.7758	900
	53	1.2377	0.7980	0.6412	900
	57	1.4229	0.9091	0.6047	400
	58	1.3508	0.8410	0.6688	900
	68	1.6195	0.9154	0.7886	900
	70	1.3016	0.9650	0.3713	36
	76	1.4143	0.8238	0.7667	900
	80	1.5701	0.9347	0.5006	225
	81	1.1602	0.7359	0.6884	400
	84	1.3013	0.9198	0.4618	225

Table 2.3: P-values and X^2 values for analyses investigating the relationship between age-0 fish density (D) and 1 of 3 eelgrass complexity measures (C) using the model $D = e^{\beta_o+\beta_C \cdot C+\beta_{C^2} \cdot C^2+\beta_Y \cdot Y+\beta_{Y \cdot C} \cdot Y \cdot C+\beta_{Y \cdot C^2} \cdot Y \cdot C^2} + \varepsilon$ where Y = year. Residuals were homogenous in all executions. Results in bold are statistically significant. NS = Newman Sound survey, FS = Fleming survey.

				$Y \cdot C^2$		$Y \cdot C$		Y	
Species	**Survey**	**C**	**DF**	χ^2	**p-value**	χ^2	**p-value**	χ^2	**p-value**
G. morhua	NS	D_P	64	2.11	0.715	2.26	0.6882	2.47	0.6499
		D_A	64	1.87	0.7594	1.84	0.7656	1.81	0.7708
		$\beta_{P/A}$	64	7.87	0.0964	7.97	0.0926	6.49	0.1656
	FS	D_P	28	***7.33***	***0.0256***	***8.31***	***0.0157***	***9.32***	***0.0095***
		D_A	28	2.17	0.3383	2.41	0.3001	2.65	0.266
		$\beta_{P/A}$	28	0.67	0.7145	1.16	0.5602	1.77	0.4137
G. ogac	NS	$\beta_{P/A}$	73	1.91	0.7526	3.04	0.5506	4.09	0.3938
U. tenuis	NS	$\beta_{P/A}$	74	1.47	0.8313	0.99	0.912	0.63	0.9599

Table 2.4: Parameter estimates and standard errors for statistically significant analyses investigating the relationship between age-0 fish density (D) and 1 of 3 eelgrass complexity measures (C) using the model $D = e^{(\beta_0+\beta_C \cdot C+\beta_{C^2} \cdot C^2)} + \varepsilon$. NS = Newman Sound survey, FS = Fleming survey. All analyses were executed with a gamma error distribution except for *U. tenuis* which used a normal error distribution.

					C		C^2		Y-Intercept	
Species	**Survey**	**C**	**DF**	**Year**	β_C	**Standard error**	β_C^2	**Standard error**		**Standard error**
G. morhua	NS	D_P	64		69.48	15.59	-24.7	5.71	-44.18	10.39
		D_A	64		1004.98	403.45	-543.62	218.62	-460.12	185.92
		$\beta_{P/A}$	64		15.25	4.30	-12.56	3.75	-0.47	1.16
	FS	D_P	9	2001	-93.32	27.41	31.13	9.88	71.08	18.84
		D_A	28		-414.02	87.35	238.58	51.13	180.63	37.06
		$\beta_{P/A}$	28		54.78	14.91	-43.12	12.06	-13.94	4.55
G. ogac	NS	$\beta_{P/A}$	73		13.95	3.83	-13.78	3.31	1.66	1.03
U. tenuis	NS	$\beta_{P/A}$	74		21.44	6.32	-26.88	7.47	0.07	1.3

Figure Captions:

Figure 2.1: Study area showing the location of the 8 eelgrass sites used in the Newman Sound survey, Bonavista Bay, Newfoundland (insert: BB-Big Brook, DS-Dockside, WR-White Rock, MI-Mistaken Cove, BC-Buckley's Cove, HC-Heffern's Cove, MC-Minchin's Cove, SB-South Broad Cove) and the 14 eelgrass sites used in the Fleming survey, northeast coast of Newfoundland (18, 32, 34, 46, 52, 53, 57, 58, 68, 70, 76, 80, 81, 84).

Figure 2.2: An illustration of the placement of on-site markers utilized in the scaling of aerial photographs of the 8 eelgrass sites in Newman Sound. Onshore markers were placed 25 m apart. A third offshore marker was placed 50 m from an onshore marker, forming a 90^{o} angle.

Figure 2.3: Relationships between age-0 Atlantic cod (*Gadus morhua*) density and eelgrass perimeter, and eelgrass area as estimated at 3 resolutions ($1m^2$, $25\ m^2$, $400\ m^2$) for 8 Newman Sound sites. Data are pooled across years 1998-2002.

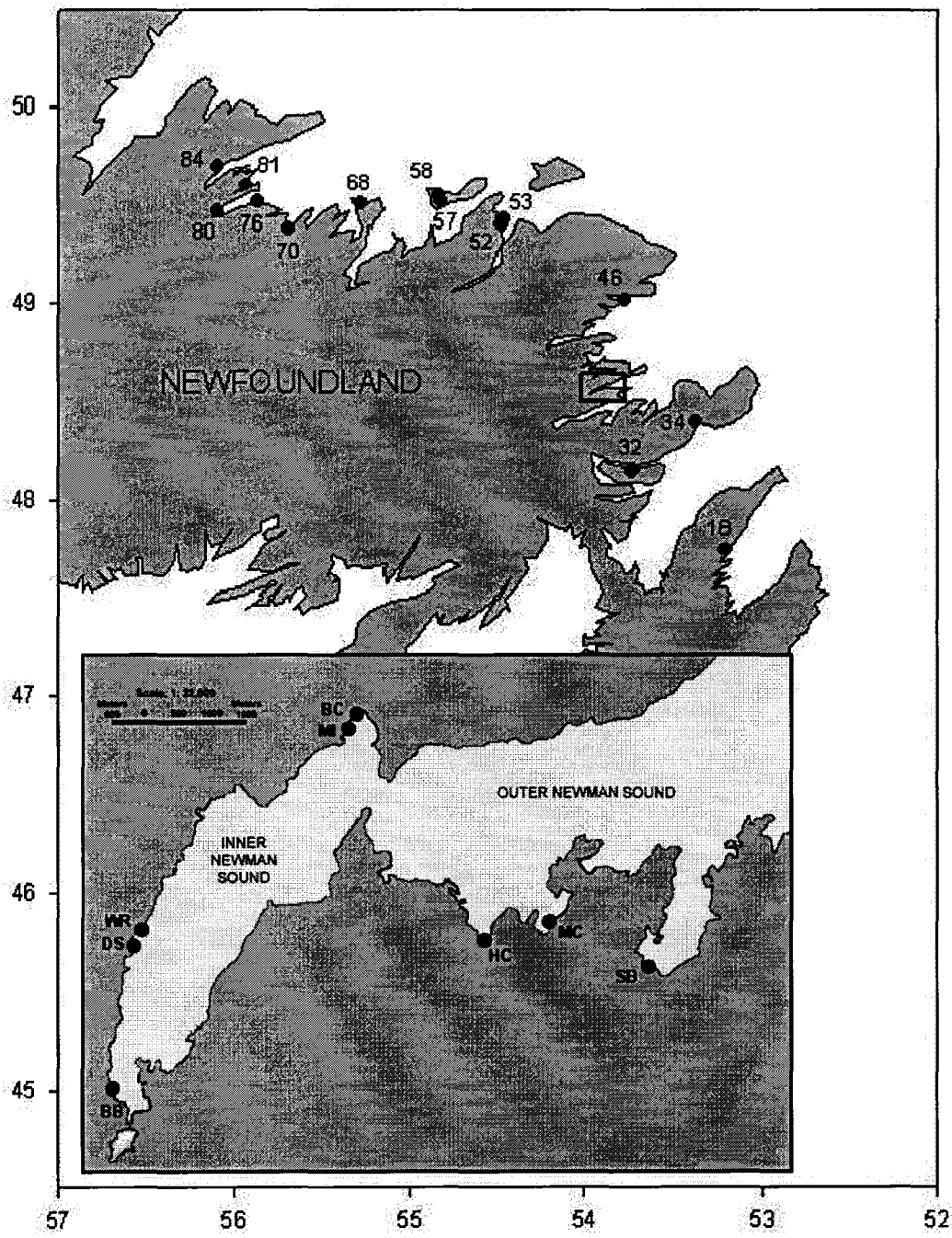
Figure 2.4: Log-log plots of perimeter vs. resolution (top panel), area vs. resolution (middle panel), and perimeter:area vs. resolution (bottom panel) for Mistaken Cove (MI).

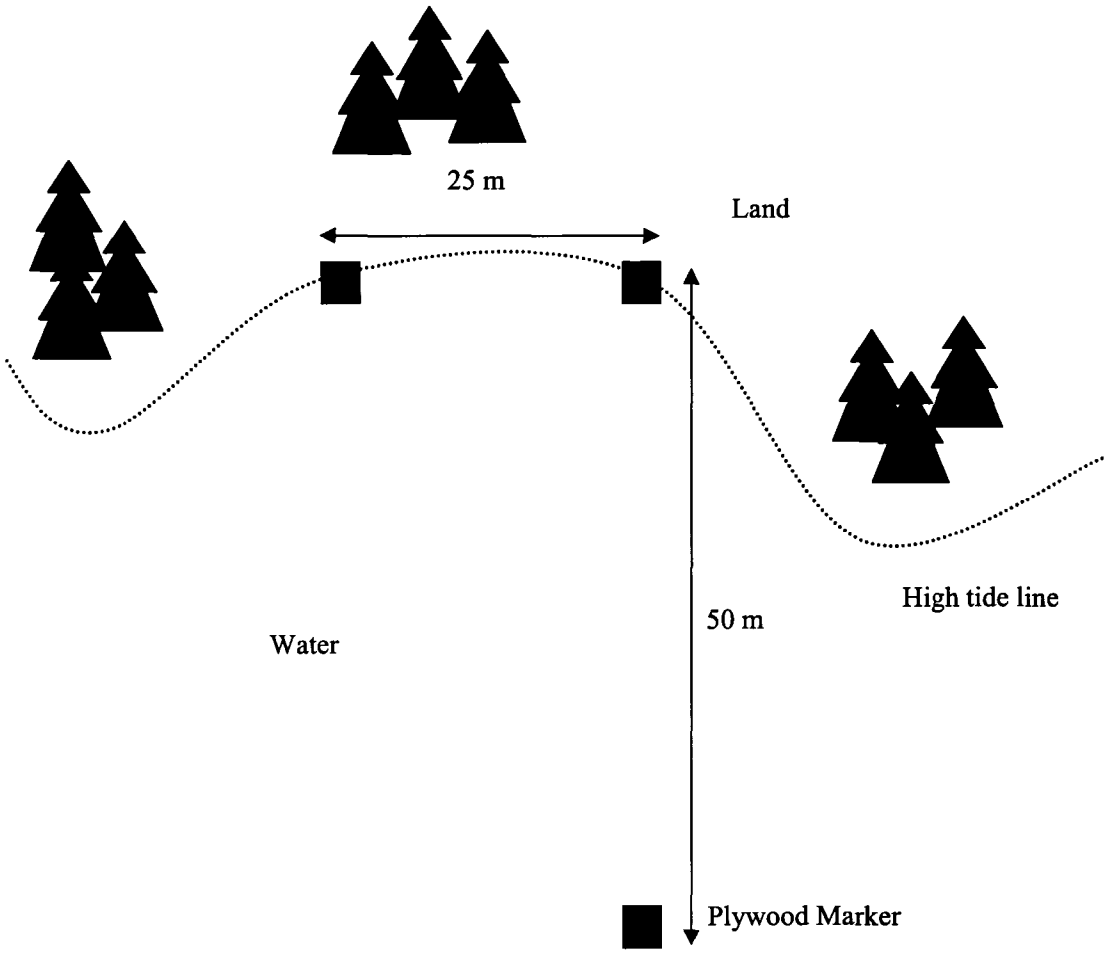
Figure 2.5: Behaviour of $\beta_{A=f(P)}$ and $\beta_{P/A}$ for varying values of D_P and D_A.

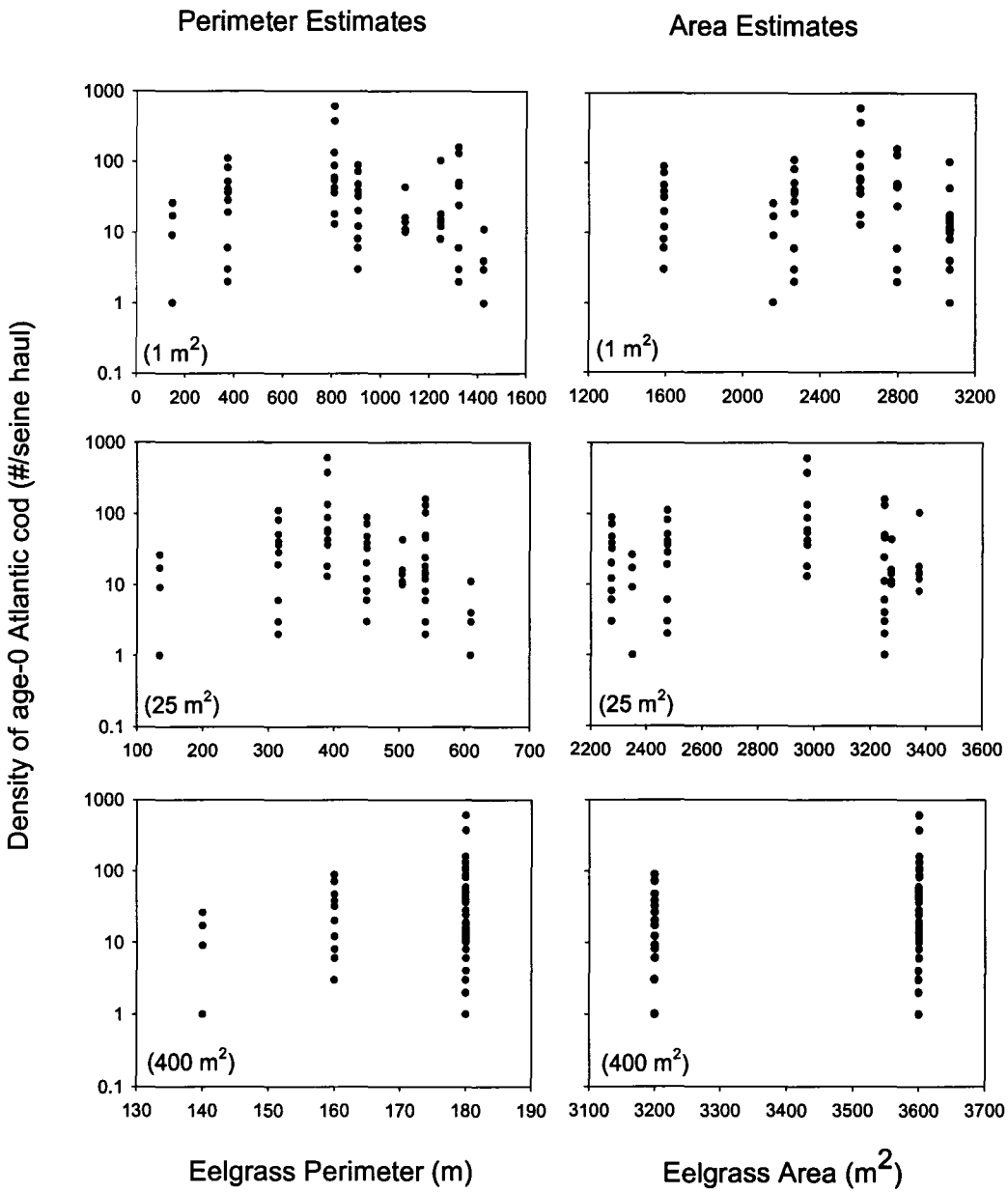
Figure 2.6: Illustration of single $|\beta_{A=f(P)}|$ representing sites of different structural complexity. While both $|\beta_{A=f(P)}|$ and $|\beta_{P/A}|$ can be determined from D_P and D_A, $|\beta_{P/A}|$ does not show the same ambiguity of $|\beta_{A=f(P)}|$. Shaded areas and lines represent eelgrass growth.

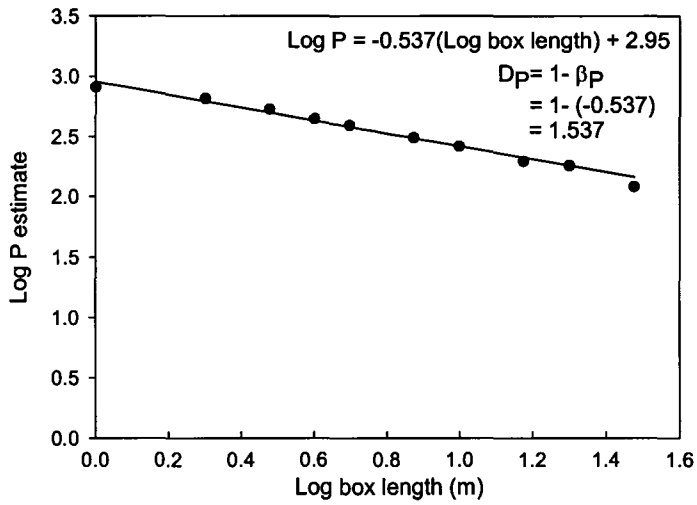
Figure 2.7: A) Relationship between age-0 Atlantic cod (*Gadus morhua*) density (D) and D_P for both the Newman Sound survey (●) and the Fleming survey (○). A significant negative quadratic relationship exists for Newman Sound data only. B) Relationship between age-0 Atlantic cod density (D) and D_A for both the Newman Sound survey (●) and the Fleming survey (○). A significant negative quadratic relationship exists for Newman Sound data (solid line), while a significant positive quadratic relationship exists for Fleming survey data (broken line).

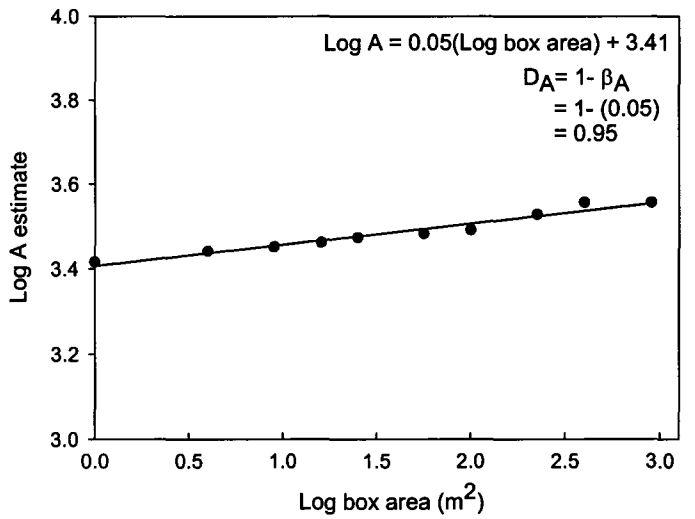
Figure 2.8: Relationship between age-0 fish densities (D) and $|\beta_{P/A}|$ for both the Newman Sound (●, solid line) and Fleming surveys (○, dashed line). Fish species are Atlantic cod (*Gadus morhua*) (top panel), Greenland cod (*G. ogac*) (middle panel), and white hake (*Urophycis tenuis*) (bottom panel). Neither *G. ogac* nor *U. tenuis* data from the Fleming surveys were available.

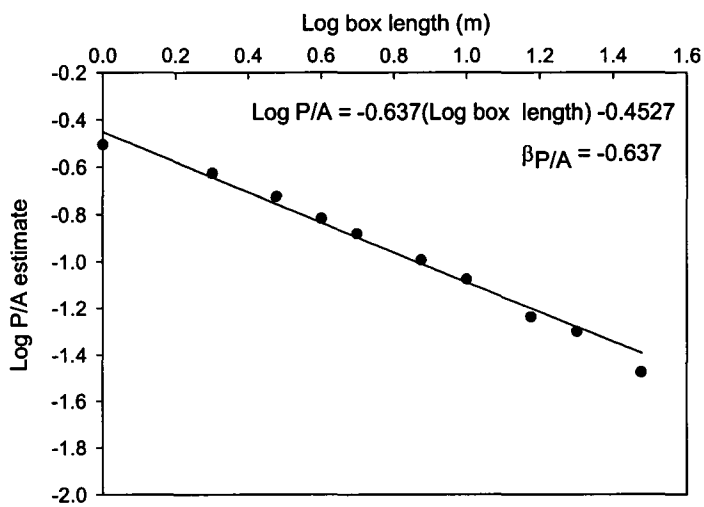

50
49
48
47
46
45
57
56
55
54
53
52
64
81
68
58
53
57
52
80
76
70
46
NEWFOUNDLAND
34
32
18
BC
OUTER NEWMAN SOUND
INNER
NEWMAN
SOUND
WR
DS
MC
HC
SB
BB

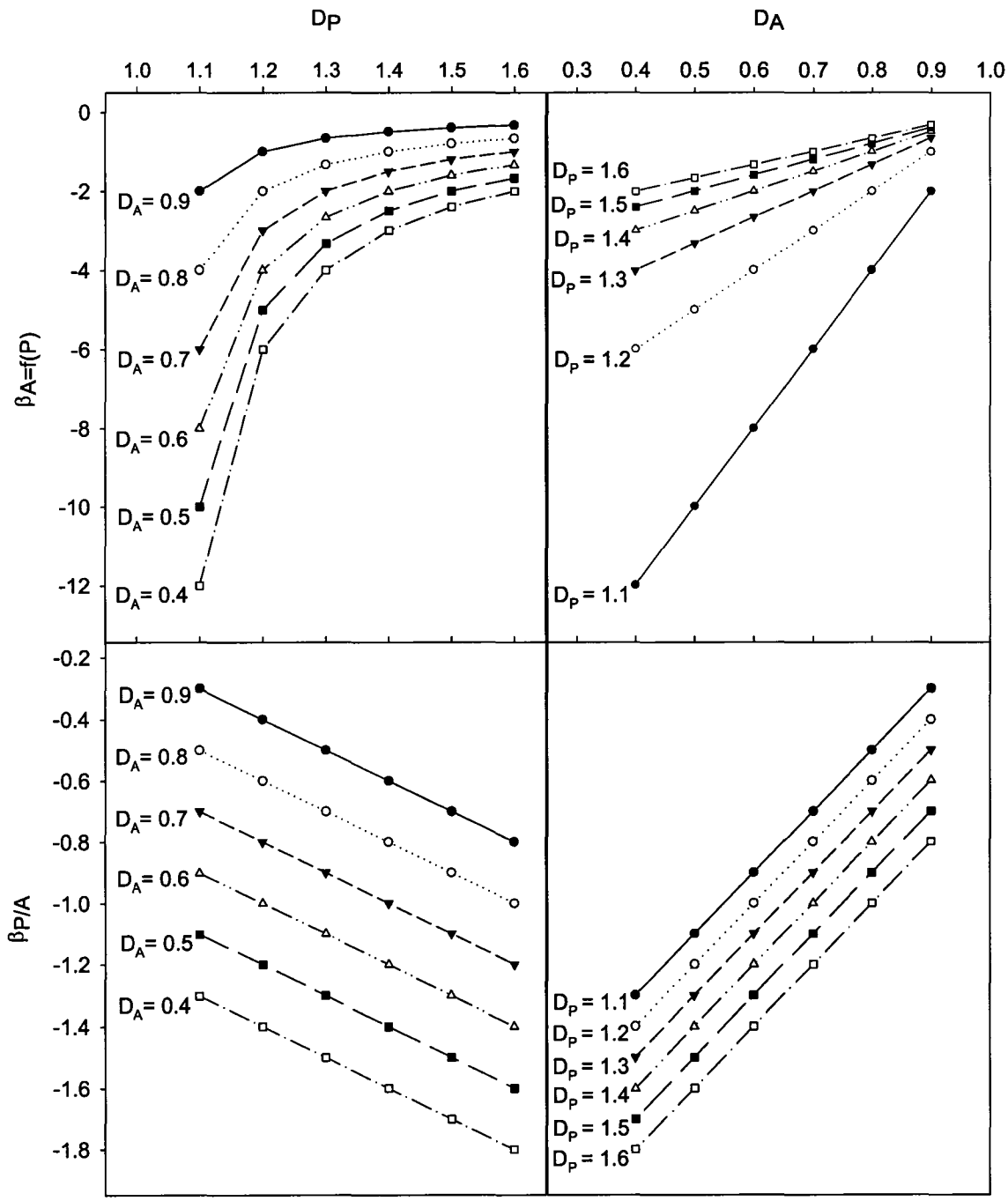

25 m
Land
High tide line
50 m
Water
Plywood Marker

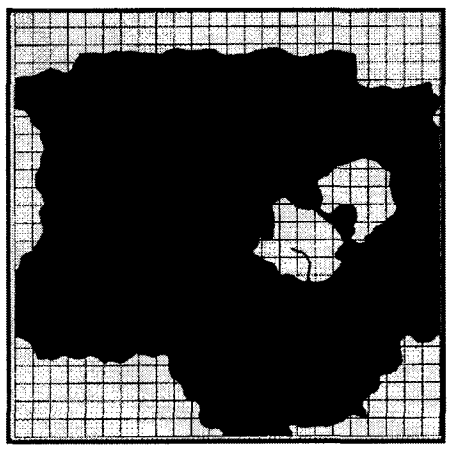

Perimeter Estimates
Area Estimates
Density of age-0 Atlantic cod (#/seine haul)
(1 m2)
(25 m2)
(400 m2)
Eelgrass Perimeter (m)
Eelgrass Area (m2)

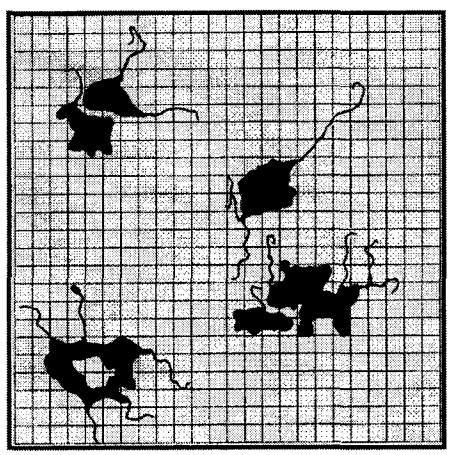

Log P = -0.537(Log box length) + 2.95
D_P= 1- β_P
= 1- (-0.537)
= 1.537
Log P estimate
Log box length (m)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6

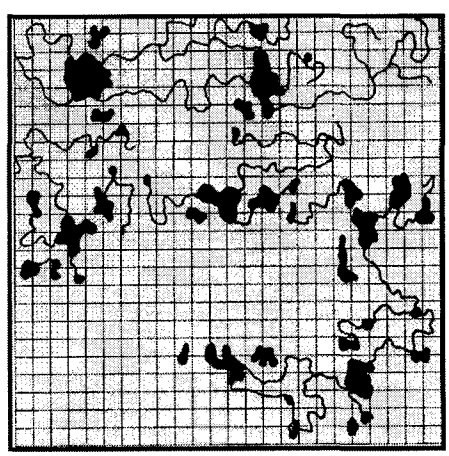

Log A = 0.05(Log box area) + 3.41
D_A= 1- β_A
= 1- (0.05)
= 0.95
Log A estimate
Log box area (m^2)
4.0
3.8
3.6
3.4
3.2
3.0
0.0 0.5 1.0 1.5 2.0 2.5 3.0

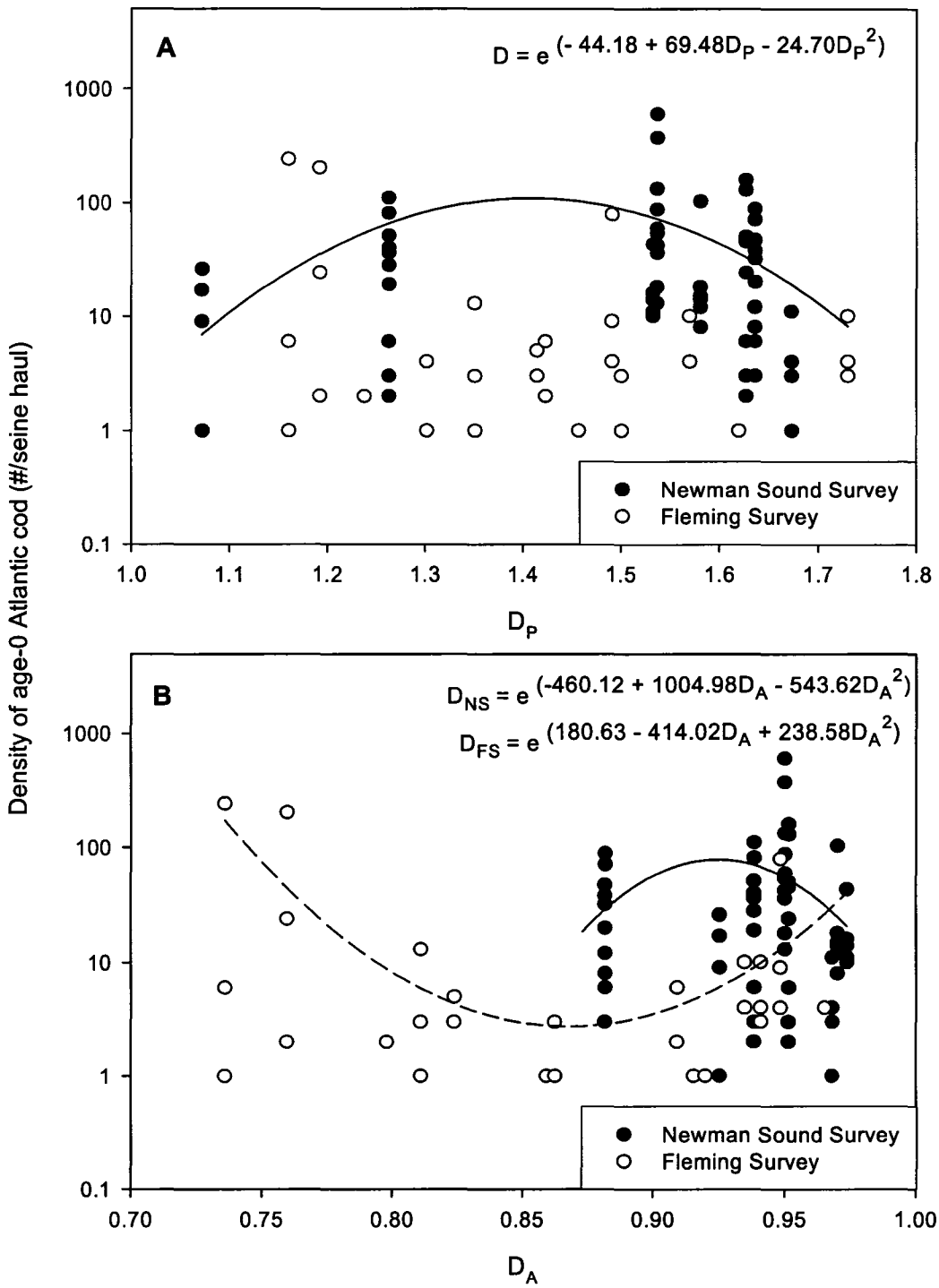

Log box length (m)
0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6
Log P/A = -0.637(Log box length) -0.4527
$\beta_{P/A}$ = -0.637
Log P/A estimate
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
-1.4
-1.6
-1.8
-2.0

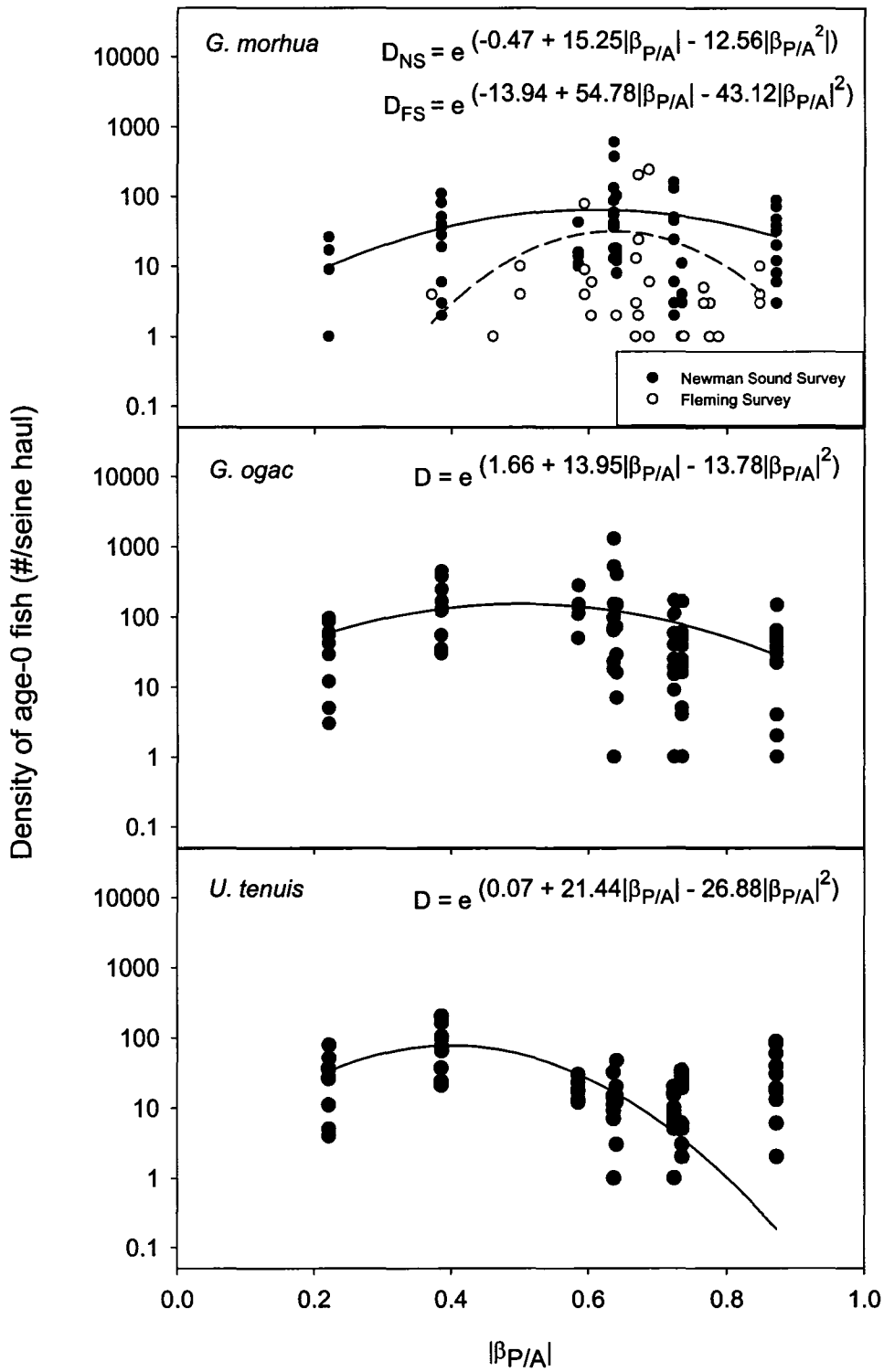

DP
DA
1.0 1.1 1.2 1.3 1.4 1.5 1.6
0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
0 -2 -4 -6 -8 -10 -12
βA=f(P)
DA= 0.9
DA= 0.8
DA= 0.7
DA= 0.6
DA= 0.5
DA= 0.4
DP = 1.6
DP = 1.5
DP = 1.4
DP = 1.3
DP = 1.2
DP = 1.1
-0.2 -0.4 -0.6 -0.8 -1.0 -1.2 -1.4 -1.6 -1.8
βP/A
DA= 0.9
DA= 0.8
DA= 0.7
DA= 0.6
DA= 0.5
DA= 0.4
DP = 1.1
DP = 1.2
DP = 1.3
DP = 1.4
DP = 1.5
DP = 1.6








A
$D = e^{(-44.18 + 69.48D_P - 24.70D_P^2)}$
Density of age-0 Atlantic cod (#/seine haul)
1000
100
10
1
0.1
1.0
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
D_P
Newman Sound Survey
Fleming Survey
B
$D_{NS} = e^{(-460.12 + 1004.98D_A - 543.62D_A^2)}$
$D_{FS} = e^{(180.63 - 414.02D_A + 238.58D_A^2)}$
1000
100
10
1
0.1
0.70
0.75
0.80
0.85
0.90
0.95
1.00
D_A
Newman Sound Survey
Fleming Survey


G. morhua
$D_{NS} = e^{(-0.47 + 15.25|\beta_{P/A}| - 12.56|\beta_{P/A}^2|)}$
$D_{FS} = e^{(-13.94 + 54.78|\beta_{P/A}| - 43.12|\beta_{P/A}|^2)}$
Newman Sound Survey
Fleming Survey
G. ogac
$D = e^{(1.66 + 13.95|\beta_{P/A}| - 13.78|\beta_{P/A}|^2)}$
U. tenuis
$D = e^{(0.07 + 21.44|\beta_{P/A}| - 26.88|\beta_{P/A}|^2)}$
Density of age-0 fish (#/seine haul)
10000
1000
100
10
1
0.1
0.0
0.2
0.4
0.6
0.8
1.0
$|\beta_{P/A}|$

Appendix A: Derivation of $\beta_{A=f(P)}$

Employing a technique by Lovejoy (1982), Wells (2002) calculated the scaling coefficient, $\beta_{A=f(P)}$, describing the relationship of how eelgrass area scales with perimeter for 8 eelgrass sites in Newman Sound, Newfoundland. Regressing one estimated variable against a second estimated variable, however, is mathematically unsound as error exists in both the x and y components. To account for this, Schneider used the definitions of perimeter and area (Table 2.1) to derive $\beta_{A=f(P)}$ as follows:

If,

$$\frac{A}{A_o} = \left(\frac{P}{P_o}\right)^{\beta_{A=f(P)}} \tag{A1},$$

$$\frac{P}{P_o} = \left(\frac{L}{L_o}\right)^{1-D_P} \text{ and } \frac{A}{A_o} = \left(\frac{L^2}{L_o^2}\right)^{1-D_A} \tag{A2, A3},$$

then,

$$\left(\frac{L^2}{L_o^2}\right)^{1-D_A} = \left[\left(\frac{L}{L_o}\right)^{1-D_P}\right]^{\beta_{A=f(P)}} \tag{A4}$$

and,

$$\left(\frac{L}{L_o}\right)^{2-2D_A} = \left[\left(\frac{L}{L_o}\right)^{1-D_P}\right]^{\beta_{A=f(P)}} \tag{A5}$$

Since the bases of each term are the same, solving for $\beta_{A=f(P)}$, yields,

$$\beta_{A=f(P)} = 2\left(\frac{1-D_A}{1-D_P}\right) \tag{A6}$$

Chapter 3: Eelgrass (*Zostera marina*) fragmentation predicts foraging success of age-0 Greenland cod (*Gadus ogac*)

3.1 Introduction

Habitat fragmentation is a central concern of conservation science in both in terrestrial and aquatic systems worldwide. Fragmented habitats have been cited as generating several deleterious ecological effects. These effects include decreased species richness and abundance (Robinson *et al.* 1992, Collinge and Forman 1998), altered population and social structures (Collins and Barrett 1997, Bruna and Kress 2002, Hanski and Gaggiotti 2004), reduced dispersal potential (Baur and Erhardt 1995), increased rates of genetic drift (Keller and Largiadèr 2003), reduced transmission of learned behaviours, and increased predation and parasitism risk at fragment edges (the edge effect) (reviewed in Ewers and Didham 2006). Response to habitat fragmentation, however, is highly variable between (Ewers and Didham 2006) and within species (Debinski and Holt 2000), and some debate remains as to the impact of habitat configuration – versus quantity - on species survival (Hanski 2005). Individual survival and fitness depend on effectively balancing conflicting demands such as foraging and predation risk (Sih 1980). There are a number of anatomical (e.g. protective armour, camouflage) and behavioural characteristics (e.g. conspecific aggregations, time-specific foraging patterns, habitat-mediated foraging) that allow animals to execute this trade-off between foraging efficiently and limiting encounters with predators.

Behavioural characteristics that facilitate this trade-off can be understood in terms of optimal foraging theory (Emlen 1966, MacArthur and Pianka 1966). While originally concerned with effects of availability, quality, and location of food on foraging behaviour, a substantial body of literature has since reported on investigations of the influence of predation risk and anti-predatory responses on foraging. Recognizing that animals often choose between habitats that differ in predation hazard and foraging return, Werner and Gilliam (1984) proposed the "minimize μ/g" rule, which states that individuals should select habitats which provide the smallest risk (measured as mortality rate, μ) for the greatest reward (growth rate, g). Gilliam and Fraser (1987) then tested a variation of this model "minimize μ/f", substituting foraging rate (f) for growth rate. Models that aim to predict the outcome of the risk/reward trade-off have been tested with success in laboratory experiments and in captive cohorts in the field (e.g. Gilliam and Fraser 1987, Nonacs and Dill 1990, Dahlgren and Eggleston 2000), however measuring site-specific predation risk as well as potential foraging opportunity in the absence of predators is difficult in open populations. While measuring both the foraging and predation components separately in the field is arduous, it is possible to measure the net result of this trade-off. Foraging success (net energy intake) is the combined outcome of risk and reward, and therefore relates directly to the optimality model, which suggests individuals with full knowledge of the alternatives within some discrete spatial area select habitat that maximize energy intake while minimizing exposure to predators (Werner and Gilliam 1984, Gilliam and Fraser 1987).

Habitat-mediated survival has been shown for juvenile (age0-1) cod (*Gadus spp.*) that occupy nearshore environments (Linehan *et al.* 2001, Laurel *et al.* 2003a,b, Gorman 2004, Gorman et al. 2006). Specifically, studies in Newfoundland waters reveal that post-settled juvenile cod utilize eelgrass (*Zostera marina*) beds as important nursery habitat (e.g. Gotceitas *et al.* 1997, Linehan *et al.* 2001, Laurel *et al.* 2003b). Eelgrass growth occurs in complex monospecific arrangements - from highly fragmented patches to extensive continuous meadows – and demonstrates a hierarchical arrangement of spatial structure, ranging from blades in shoot groups (centimetres), to shoot groups in patches (meters), to patches in meadows (kilometres) (Robbins and Bell 1994). In addition to naturally complex spatial formations (Robbins and Bell 1994), eelgrass landscapes are susceptible to fragmentation via anthropogenic alteration (Fonseca 1992). The spatial arrangement of seagrass habitats (co-occurrence of vegetated and non-vegetated substrate) is considered an important factor influencing many aquatic faunal species (e.g. Heck and Orth 1980, Orth *et al.* 1984, Irlandi *et al.* 1995, Barberá-Cebrián *et al.* 2002, Hyndes *et al.* 2003) including cod (Chapter 2).

I have demonstrated (Chapter 2) that eelgrass spatial complexity (as measured by a fractal coefficient) dictates a parabolic distribution of age-0 juvenile fish density among species common in Newfoundland coastal waters, including Atlantic cod (*G. morhua*), Greenland cod (*G. ogac*), and white hake (*Urophycis tenuis*). Juvenile Greenland cod demonstrated the strongest relation of density to complexity, however their ecology has received little attention (but see Laurel *et al.* 2003a,b, 2004). Wells (2002) suggested that maximum fish densities at sites of intermediate eelgrass spatial complexity might impart

an optimal trade off in food accessibility and predator avoidance – the Intermediate Optimum Hypothesis (IOH).

In this study I investigate whether or not a trade-off in foraging and predation risk, as measured by individual foraging success and in accordance with IOH, is responsible for the parabolic relationship between age-0 Greenland cod density and eelgrass complexity, as determined by a fractal measure including edge convolution and area fragmentation ($\beta_{P/A}$). Specifically, I determine how foraging success differs at sites of different structural complexities. Furthermore, I predict the relationship between foraging success and $\beta_{P/A}$ from both the density-$\beta_{P/A}$ relationship and the assumption that density of age-0 Greenland cod will increase with more favourable foraging-predation risk tradeoffs in order to maximize foraging success. If a habitat mediated balance in foraging and predator evasion is responsible for the relation of density to eelgrass complexity, then I expect foraging success of age-0 Greenland cod to be greatest in fish caught at intermediate complexities.

3.2 Theory

Using data from two surveys of different geographical extent, I found that densities of age-0 juvenile gadids are a function of eelgrass structural complexity, as measured by $|\beta_{P/A}|$ (Chapter 2). Specifically, the density distribution of age-0 Greenland cod with respect to $|\beta_{P/A}|$ was described by the negative parabolic equation:

$$D = e^{\left(13.95|\beta_{P/A}| - 13.78|\beta_{P/A}|^2 + 1.66\right)} \tag{3.1}$$

where D is Greenland cod density (number of individuals/seine haul), and $\beta_{P/A}$ is a dimensionless scaling coefficient describing how the perimeter:area of an eelgrass site changes with scale.

Wells (2002) suggested that this parabolic relationship results from a trade-off in feeding opportunity and predator evasion, such that sites of intermediate complexity provide sufficient protective cover along with opportunity to forage over barren areas (Intermediate Optimum Hypothesis - IOH). A measure of the effects of a trade-off affecting risk-sensitive foraging is foraging success. Central to the IOH then, is the assumption that density (D) will be high when there is opportunity for high foraging success (FS, food weight/fish weight x 100%) and hence, D is a function of FS:

$$D = f(FS) \tag{3.2}$$

Using data collected on density of age-0 Greenland cod and the foraging success of individuals, I determined the relationship between these two variables. Because equations 3.1 and 3.2 share a common variable (density), it is possible to solve for the relationship between foraging success (FS) and $|\beta_{P/A}|$:

$$FS = f(|\beta_{P/A}|) \tag{3.3}$$

To test the fit of this theoretical prediction, I compared its parameter to those of a model fit from empirical data.

3.3 Methods

3.3.1 Study Area

Newman Sound is a protected fjord adjacent to Terra Nova National Park, within southwestern Bonavista Bay, Newfoundland and Labrador, Canada (Figure 3.1). The sound extends approximately 45 km^2 and is divided into two basins by a sill located ~ 7 km from the head of the sound. Average tidal amplitude is low (1-1.5 m). The substrate and associated vegetative cover in the nearshore environment (0-15 m depth) is varied, however eelgrass, *Zostera marina,* is the dominant vegetation. Found primarily along the western and southern coastlines of the sound, eelgrass occurs on mud, sand, and gravel substrates, and is restricted to areas of seabed less than 6 m deep.

I selected 4 sites (Figure 3.1) based on the presence and spatial configuration of eelgrass habitat. Specifically, I selected sites representing different eelgrass complexities and different points along the parabolic relationships that describe how juvenile Greenland cod density varies with respect to eelgrass complexity.

3.3.2 Nearshore Fish Community Surveys and Sampling

The nearshore fish communities at all sites were sampled on a biweekly schedule, at the beginning, middle, and end of September 2004. Each site was sampled within two hours of diurnal low-tide via a 25 m demersal beach seine. Sites were never sampled within an hour of dusk to eliminate the crepuscular effects on fish distribution and behaviour. The seine was deployed 55 m from shore from a 6 m boat, and was retrieved by two individuals on shore standing 16 m apart. Pulled along the seafloor, the seine samples the bottom 2 m of the water column, covering approximately 880 m^2 of demersal

habitat. Deployed in this manner, SCUBA observations have demonstrated that the seine catches 95% of the fish fauna in its path and induces negligible mortality (Gotceitas *et al.* 1997). A more detailed description of the seine's construction, deployment, and retrieval is located in Schneider *et al.* (1997).

Collected fish were transferred to containers of seawater, counted, measured, and identified. Fish were measured to standard length (most anterior point to caudal peduncle). Juvenile cod were aged by applying previously established age-length relationships (Gregory *et al.* 2006). A sample of up to 10 age-0 Greenland cod individuals were killed from each site biweekly for stomach content analysis in the lab. All remaining fish were released to their site of capture following sorting

Sampled fish were killed by a blow to the head and were fixed in a 4% buffered formalin-seawater solution for 48 hours. Following fixation, samples were rinsed with freshwater and transferred to 95% ethanol for long term preservation and storage.

3.3.3 Age-0 Greenland Cod Foraging Success

For each site and date, I used total gut content weights as an estimate of foraging success. This measure assumes no difference in food quality, handling time, or capture efficiency, which may influence energetic gain. Preserved fish were soaked in freshwater for 2 hours prior to dissection to remove ethanol from tissues. A 2 hour period was selected as preliminary analysis demonstrated this was the interval after which fluctuation in weight measurement (due to preservative) was eliminated. Following the 2 hour period, fish were removed from water and blotted dry. Standard lengths were

measured to the nearest 0.02 millimetre using Vernier callipers. Fish were weighed (wet weight) on an analytical balance to the nearest 0.001 g and tagged through the buccal cavity and opercular opening with a unique identifier.

To remove each stomach, I severed the pharyngeal isthmus and made an incision on the ventral surface from the isthmus posterior to the anus. The entire digestive tract (anterior of the esophageal sphincter to the anus) was excised and the stomach isolated (through the esophageal sphincter to the narrowing, anterior of the pyloric caeca). The full stomach was blotted lightly to remove residual moisture from the body cavity and weighed. The stomach was opened and all contents were placed in a plastic cryovial labelled with the appropriate unique identifier. Stomachs were rinsed with 95% ethanol and stomach contents were stored for future analysis. Empty stomachs were blotted dry and weighed.

Stomach content weight (i.e. food weight, FW) was determined as follows:

$$FW = FSW - ESW \tag{3.4}$$

where FSW is the full stomach weight and ESW is the empty stomach weight. Foraging success (FS) was expressed as the percentage of total fish mass that was attributed to food:

$$FS = \left(\frac{FW}{TW}\right) \times 100\% \tag{3.5}$$

where TW is the total weight of each fish. Following the removal of the stomachs all fish were re-stored in a 95% ethanol solution. Preliminary analysis determined that empty stomach weight scaled isometrically with total fish weight with an exponent of

0.9938 as estimated by log-log regression (standard error = 0.03348, n = 123). In addition, there were no size differences (TW) among fish from different sites (Mean ± SD for each site: Big Brook 4.98 ± 1.97 g, Heffren's Cove 4.82 ± 2.62 g, Mistaken Cove 4.91 ± 2.91 g, South Broad Cove 5.12 ± 2.48 g. One-way ANOVA: $F_{3,119} = 0.0857$, p = 0.968, n = 123).

3.3.4 Relating age-0 Greenland cod density to foraging success and $\beta_{P/A}$

I investigated the relationship between individual foraging success and age-0 Greenland cod density, when present, using data from the September 2004 survey. Densities were computed as number of fish/seine haul (number of fish/880m^2). This relationship was examined via an exploratory approach using a software package (SigmaPlot 7.0) with a multitude of curve-fitting functions. I used both fish density and the natural log of fish density as possible y-variables in the exploratory analysis. The suitability of several fitted functions were evaluated by examining the p-values of parameter co-efficients (tolerance for type I error at $\alpha = 0.05$). SigmaPlot 7.0 software evaluates functions based on a normal error distribution, hence, residuals for each model were examined for homogeneity, normality, and independence. Once $D = f(FS)$ was determined, I used this function and the relationship that describes how Greenland cod density changes with $|\beta_{P/A}|$ (equation 3.1) to solve $FS=f(|\beta_{P/A}|)$. Note that while I expected variance in FS to be explained by $\beta_{P/A}$ (via D) there is no necessary reason that the coefficients from $FS = f(D)$ and $D=f(\beta_{P/A})$ should predict the coefficients in $FS = f(\beta_{P/A})$.

In order to compare the predicted $FS=f(|\beta_{P/A}|)$ to empirical data, I used data from the September 2004 survey to investigate the relationship between the foraging success of age-0 Greenland cod and the structural complexity of the eelgrass site at which they were caught. The validity of the predicted function was tested by analyzing the empirical data in a model with the same terms and link function. Analyses were performed with a normal error distribution within the framework on the generalized linear model (McCullagh and Nelder 1987), and residuals were examined for the assumptions of homogeneity, independence, and normality. If a normal error distribution was inappropriate, a gamma error structure was used. Generalized linear model analyses were executed using the Gen mod procedure in SAS statistical software (1988). The tolerance of type I error was $\alpha = 0.05$.

3.4 Results

3.4.1 Density of age-0 Greenland cod and foraging success

Age-0 Greenland cod density increased significantly with foraging success ($F_{1,121} = 10.2282$, $p = 0.0018$, Table 3.1, Figure 3.2) as best described by a function of the following form:

$$y = a\ln(x - x_o) \qquad 3.6$$

In this relationship, a is a co-efficient (same dimensions as y) that describes the degree of vertical stretching or compression, and x_o translates the function along the x-

axis. Specifically, the model that described how density changed with foraging success was:

$$\ln D = 1.789 \ln(x - (-5.910)) \tag{3.7}$$

Which can be expressed as,

$$D = e^{(1.789 \ln(FS + 5.910))} \tag{3.8}$$

(a: $t_{1,121} = 9.515$, $p < 0.0001$, x_o: $t_{1,121} = -3.0461$, $p = 0.0028$).

3.4.2 Solving $FS = f(|\beta_{P/A}|)$

Using equations 3.1 and 3.8 and algebraic substitution, I determined the theoretical relationship between foraging success of age-0 Greenland cod and eelgrass structural complexity, as measured by $|\beta_{P/A}|$ as follows:

$$D = e^{(1.789 \ln(FS + 5.910))} \tag{3.8}$$

using properties of exponents, is equivalent to

$$D = \left(e^{\ln(FS + 5.910)^{1.789}} \right) \tag{3.9}$$

and therefore,

$$D = (FS + 5.910)^{1.789}. \tag{3.10}$$

Because density relates to $|\beta_{P/A}|$ as

$$D = e^{\left(13.95|\beta_{P/A}| - 13.78|\beta_{P/A}|^2 + 1.66\right)} \tag{3.1}$$

it is possible to substitute equation 3.10 for D,

$$(FS + 5.910)^{1.789} = e^{\left(13.95|\beta_{P/A}| - 13.78|\beta_{P/A}|^2 + 1.66\right)} \tag{3.11}$$

Further simplifying

$$FS + 5.910 = \left(e^{\left(13.95|\beta_{P/A}| - 13.78|\beta_{P/A}|^2 + 1.66\right)} \right)^{\frac{1}{1.789}}, \quad 3.12$$

$$FS + 5.910 = e^{\left(7.797|\beta_{P/A}| - 7.703|\beta_{P/A}|^2 + 0.928\right)}, \quad 3.13$$

reveals,

$$FS = e^{\left(7.97|\beta_{P/A}| - 7.703|\beta_{P/A}|^2 + 0.928\right)} - 5.910. \quad 3.14$$

This relationship describes a negative (downward facing) parabola, whereby maximum foraging success occurs at sites of intermediate structural complexity, $|\beta_{P/A}|$.

3.4.3 Evaluating the empirical relationship between foraging success and $|\beta_{P/A}|$

In accordance with the derived relationship (equation 3.14), empirical data of age-0 Greenland cod foraging success was compared to the structural complexity measure $|\beta_{P/A}|$ in a model containing a quadratic term, and a natural log link expressing a multiplicative effect of habitat variation on FS:

$$FS = e^{\mu} + \varepsilon \quad 3.15a$$

$$\mu = \beta_o + \beta_C \cdot C + \beta_{C^2} \cdot C^2 \quad 3.15b$$

where C = the complexity measure, $|\beta_{P/A}|$. Use of a normal error distribution produced non-normal and slightly heterogeneous residuals. Execution of the model with a gamma error distribution eliminated these problems. The foraging success-$|\beta_{P/A}|$ relationship

demonstrated a significant negative (downward opening) quadratic (β_C: $X^2_{1,121} = 16.47$, $p < 0.0001$, β_C^2: $X^2_{1,121} = 17.80$, $p < 0.0001$, Table 3.1, Figure 3.3):

$$FS = e^{\left(6.6858|\beta_{P/A}| - 6.1641|\beta_{P/A}|^2 - 0.3065\right)} \quad 3.16$$

This relationship, in accordance with the derived relationship (equation 3.13), reveals that maximum foraging success occurs at sites of intermediate values of $|\beta_{P/A}|$.

3.4.4 Comparing the derived and empirical relationship between foraging success and $|\beta_{P/A}|$

Both the derived theoretical and empirical relationships between foraging success of age-0 Greenland cod and $|\beta_{P/A}|$ demonstrate consistent, negative (downward opening), quadratic functions. However, the theoretical relationship included an extra constant term (-5.910) which elongates the parabola along the y-axis by altering the y-intercept. To assess the shape of the predicted relationship with respect to the empirical data set, the derived function was solved such that it passed through the co-ordinate corresponding to the mean x and mean y values, 0.5523, and 3.3260 (%), respectively, and solved for a new constant term, c:

$$FS = e^{\left(7.797|\beta_{P/A}| - 7.703|\beta_{P/A}|^2 + c\right)} \quad 3.17$$

Substituting in the mean values of foraging success and $|\beta_{P/A}|$,

$$3.3260 = e^{\left(7.797 \cdot 0.5523 - 7.703 \cdot 0.5523^2 + c\right)} \quad 3.18$$

simplified further,

$$\ln(3.3260) = 4.3063 - 2.3497 + c \quad 3.19$$

$$1.2018 = 1.9566 + c \quad 3.20$$

$$c = -0.7548 \quad 3.21$$

Therefore, when fit through the grand mean of the empirical data set, the theoretical relationship is:

$$FS = e^{\left(7.797|\beta_{P/A}| - 7.703|\beta_{P/A}|^2 - 0.7548\right)} \quad 3.22$$

This analysis demonstrates that the theoretical parameter co-efficients easily fall within the 95% confidence intervals estimated by the empirical model ($|\beta_{P/A}|$: theoretical = 7.797, empirical estimate = 3.598 - 9.774, computed from 6.6858 in equation 3.16. $|\beta_{P/A}|^2$: theoretical = -7.703, empirical estimate = -8.901 - -3.427, computed from 6.1641 in equation 3.16. Y-intercept: theoretical = -0.7548, empirical estimate = -1.068 - 0.4550 computed from 0.3065 in equation 3.16).

3.5 Discussion

I have shown that age-0 Greenland cod foraging success is parabolically related to eelgrass complexity, as determined by a fractal measure of edge convolution and area fragmentation ($|\beta_{P/A}|$). Specifically, sites of intermediate eelgrass complexity support fish with the greatest foraging success, as estimated by stomach fullness, consistent with Wells' (2002) intermediate optimum hypothesis. In addition, I have demonstrated that the foraging success-$|\beta_{P/A}|$ relationship for age-0 Greenland cod can successfully be predicted from previously described density-$|\beta_{P/A}|$ relations as well as foraging success-density relations.

Factors that affect foraging success have been the focus of numerous, varied investigations. Foraging success is used because it relates directly to energy intake, which contributes ultimately to individual fitness. Furthermore, this measure is particularly appropriate for assessing potential fitness in juveniles in a number of ways. Fitness cannot be assessed via reproductive output in these individuals, as they are not mature and producing offspring. Likewise, foraging success can act as a proxy for fitness since few activities that limit foraging ability but may otherwise increase fitness, such as courting or mating, occur at this life-stage. Interpreted alternately, foraging success also indicates fitness, as it directly assesses the outcome of foraging-predation avoidance trade-offs, assuming the animals are behaving optimally. In this way assessing foraging success allows one to assess outcomes of behaviours that influence fitness on a finer timescale than indicators such as reproductive output. This is in contrast to such measures as reproductive output, which may be difficult to determine and represents the combined influence of many behavioural outcomes (Lima 1998). Additionally, unlike measuring separate components of this trade-off, foraging success incorporates the non-lethal elements of predation, which may not be discernible from estimates of predation rates (Lima 1998).

Several studies have investigated the influence of seagrass fragmentation on resident biota, however these studies often use metrics to describe habitat that are scale dependent, are patch-specific characteristics, do not quantify landscape shape and arrangement, or are compiled into poorly-understood indices. The measured components used to assess seagrass complexity include patch size (Irlandi 1997), number of patches

(Salita *et al.* 2003), shoot density (Bell and Westoby 1986a, Graham et al. 1998), biomass (Adams 1976), percent cover (Heck and Orth 1980, Salita *et al.* 2003), and leaf height (Bell and Westoby 1986b). Additionally, these studies often focus on abundance and distribution patterns rather than factors affecting survival or fitness. Studies that have examined seagrass fragmentation and survival have had varying outcomes. For example, Irlandi (1997) determined that survivorship of an infaunal bivalve (*Mercenaria mercenaria*) decreased as natural seagrass patch size decreased. However, in a subsequent study using artificial eelgrass patches, Irlandi *et al.* (1999) suggested that this difference could be attributed to variability in shoot density, and below-ground biomass. Similarly, in a study concerning juvenile blue crab survival and abundance, Hovel and Lipcius (2002) found that survival was reduced in isolated patches, and decreased with shoot density, the later which was attributed to high incidents of predation by older conspecifics, but was unaffected by patch size. Patch size, however, did affect tethered juvenile cod survival, as Laurel *et al.* (2003a) found that predation rates were negatively correlated with the size of artificial eelgrass patches.

A number of investigators have recognized that fragmentation occurs at a landscape scale (reviewed in Ewers and Didham 2006), and so there has been a call to move from individual patch-studies to patches in landscapes (Frost *et al.* 1999, Hokit *et al.* 1999, Bell *et al.* 2001, Jackson *et al.* 2006). Despite this, surprisingly few studies in the seagrass literature have tackled this challenge. Those that have examined fragmented seagrass landscapes have used composite measures to assess multiple aspects of a habitat (Turner *et al.* 1999, Salita *et al.* 2003, Jackson *et al.* 2006). Composite measures, such as

those derived from principle component analysis (PCA) can be useful in exploratory analysis, however these indices pose several challenges to interpretation. For example, composite measures may obscure the underlying mechanism driving the pattern of fragmentation. In addition, the biological interpretation of the composite measure may be inconsistent between readers. Finally, patterns associated with composite measures cannot be compared across studies since the relative influence of the components may shift from time to time or place to place.

In Chapter 2, I have demonstrated that a single measure of habitat heterogeneity, determined on a landscape scale and based on spatial patterning, can be obtained using the multi-scale technique, fractal analysis. Fractals are scaling co-efficients which can describe how a habitat characteristic's magnitude changes with scale of measurement, and therefore can be used to quantify habitat spatial heterogeneity and shape. Given the convoluted and irregular pattern of eelgrass growth, as well as the potential biological importance of barren and vegetated areas to faunal inhabitants, the use of fractal geometry to describe eelgrass site shape complexity is biologically appropriate (Davidson 1998, Gustafson 1998, Bogaert 2003). I have found that the scaling co-efficient, $\beta_{P/A}$, which describes how the perimeter:area of a habitat changes with scale, describes eelgrass site complexity. Specifically, this single measure assesses the degree of eelgrass perimeter convolution and area fragmentation, and therefore is advantageous compared to composite measures that may be difficult to interpret. Another advantage of a single, fractal measure is that it provides a quantitative estimate of spatial heterogeneity in any two-habitat system. For example, in aquatic habitats this could include macro-algae

amongst cobble, or even cobble/sand habitats, and in terrestrial landscapes, vegetated/open habitats such as mixed forest and grassland. In this way, quantifying habitat fragmentation by $\beta_{P/A}$ allows cross-species and cross-community comparisons of the effects of habitat shape complexity.

In this study, I successfully predicted that eelgrass site fragmentation, as indicated by $\beta_{P/A}$, would influence the foraging success of age-0 Greenland cod. Because foraging success depends upon such things as food accessibility and predation risk, one can hypothesize which factors might perturb the predicted relation between foraging success and $|\beta_{P/A}|$, and how these factors might affect the shape of the curve. Foraging success is largely dependent upon food availability and thus increasing or decreasing food supply may influence the foraging success-$|\beta_{P/A}|$ relation in a number of ways. For example, if we assume no relationship between the zooplankton preyed upon by age-0 Greenland cod and eelgrass complexity, an increase in prey across all eelgrass sites might be expected to result in a positive (upward) translation along the y-axis. Alternatively, an increase in food abundance might also result in a broader parabolic relation such that sites of low $|\beta_{P/A}|$ would exhibit an increase in food *accessibility*, and sites of high $|\beta_{P/A}|$ would provide a magnified reward and reduced μ/f, despite the elevated levels of predation in highly fragmented locations. Likewise, altering the predator abundance at eelgrass sites would also affect Greenland cod foraging success, and therefore the relationship between foraging success and $|\beta_{P/A}|$. For example, an increase in predators might be expected to cause a negative (downward) translation in the parabolic relation along the y-axis. Furthermore, a large increase in predator density across sites might elevate the risk at

sites of intermediate to high $|\beta_{P/A}|$, thus overwhelming any increase in foraging benefit associated with these sites. In this scenario, the foraging success-$|\beta_{P/A}|$ relation might be expect to be negatively displaced, and have a negative, linear slope.

This study, like optimal foraging theory, provides a predictive model that can be verified using experimental data. In their review on species responses to habitat fragmentation, Ewers and Didham (2006) noted a lack of predictive studies, despite a substantial theoretical literature on fragmentation (Debinski and Holt 2000), and cite the ability to predict effects of fragmentation as one of the most important problems to be tackled in the future. Furthermore, my study uses a multi-scale measure of fragmentation ($\beta_{P/A}$) that describes landscape shape. Specifically, $\beta_{P/A}$ describes both the perimeter convolution and area fragmentation of any two-component habitat system, and therefore allows for comparisons of fragmentation effects across systems. The ability to compare patterns across studies will certainly enhance our understanding of, as well as better enable predictions of species responses to fragmentation.

Consistent with the intermediate optimum hypothesis, this study demonstrates that eelgrass habitat shape influences the success of age-0 Greenland cod. In addition to uncovering more information about the ecology of this poorly understood species, the resulting knowledge addresses the query that spatial configuration of habitat, rather than quantity, may not have a major effect on survival (Harrison 2006). Therefore, this study provides further support for the incorporation of spatial theory when identifying and protecting habitat of conservation concern.

Furthermore, this study strikes a balance between the call to address the behavioural mechanisms that drive species' responses to fragmented habitats (Ewers and Didham 2006) and assessing these responses at an appropriate scale. While truly mechanistic studies are best accomplished via controlled laboratory manipulations of microcosms, it may be difficult to replicate the influence of landscape-scale fragmentation. By measuring foraging success as the outcome of a risk-reward trade-off, this study investigates a behavioural response at an appropriate scale. Because a trade-off in foraging efficacy and predator avoidance appears to drive distribution of individuals, this study further suggests that a parabolic relationship between density and fragmentation may apply to any species that uses habitat to offset predation risk while providing open areas in which to forage.

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Table 3.1: Parameter estimates and standard errors for variables in the statistically significant relationships describing age-0 Greenland cod density (D) with respect to foraging success (FS), and foraging success with respect to eelgrass site complexity (C) as measured by $|\beta_{P/A}|$. The analyses were executed with a normal error distribution and a gamma error distribution, respectively

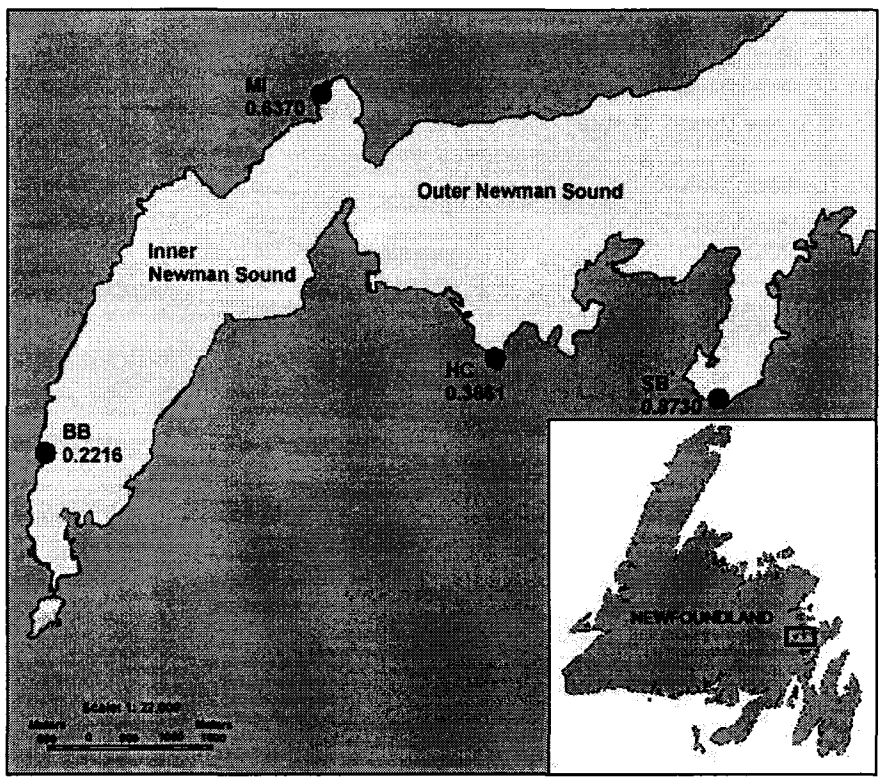
model	df	variable	parameter estimate	standard error
$D = e^{(a \ln(FS - FS_O))}$	122	a	1.789	0.188
		FS_o	-5.910	1.940
$FS = e^{(\beta_o + \beta_C \cdot C + \beta_{C^2} \cdot C^2)}$	122	β_o	-0.3065	0.3886
		C	6.6858	1.5755
		C^2	-6.1641	1.3965

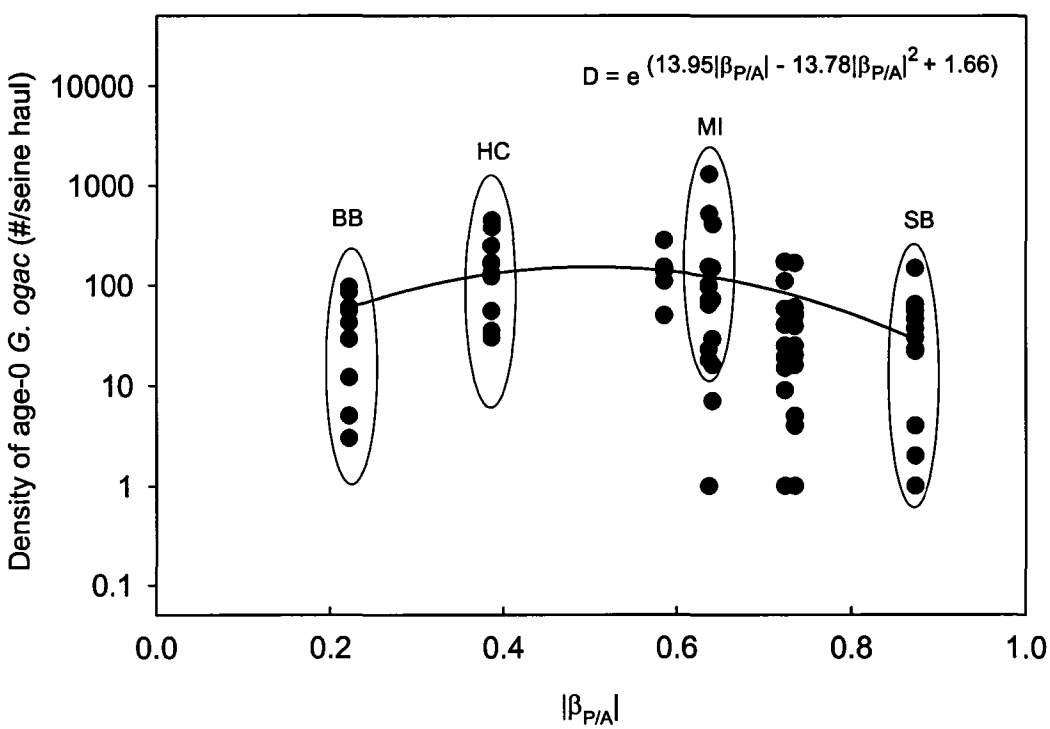
Figure Captions

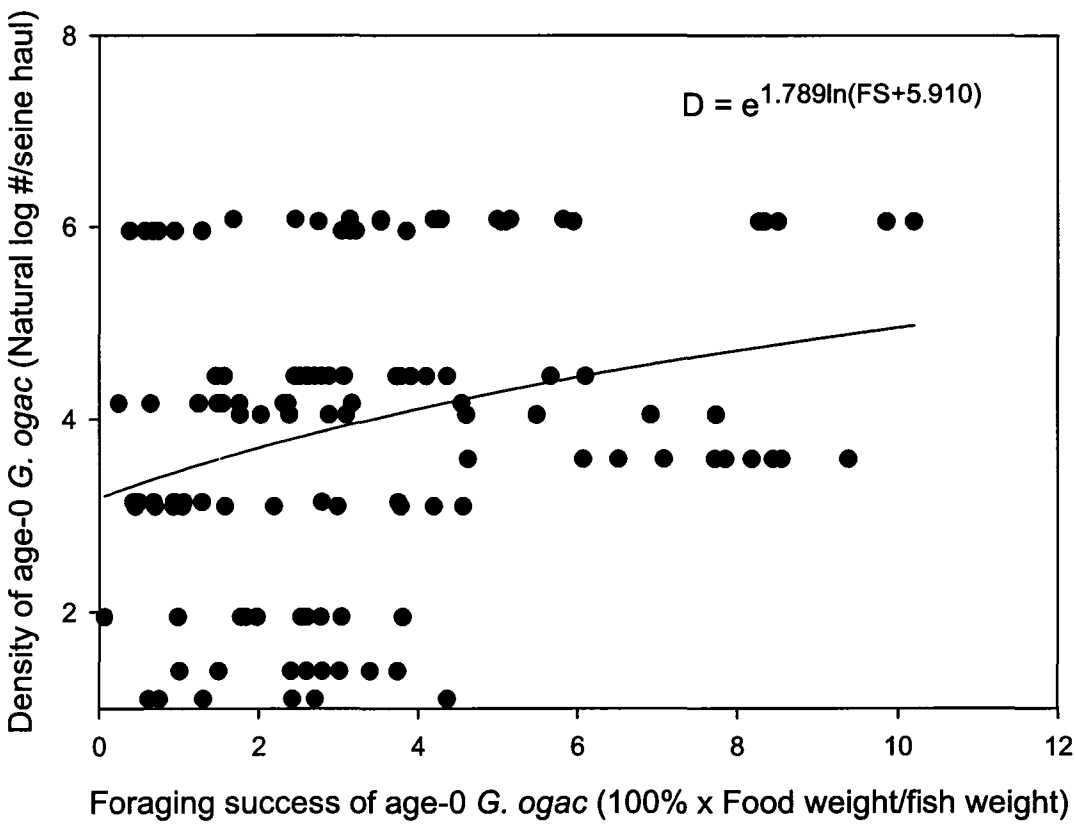
3.1 Top panel: The location and $|\beta_{P/A}|$ values of the 4 eelgrass sites in Newman Sound, Bonavista Bay, Newfoundland, used to collect age-0 Greenland cod (*G. ogac*) for foraging success analysis (BB-Big Brook, MI-Mistaken Cove, HC-Heffern's Cove, and SB-South Broad Cove). Bottom panel: The relationship between age-0 Greenland cod densities (D) and $|\beta_{P/A}|$ for 8 eelgrass sites in Newman Sound. The sites selected to assess foraging success are indicated.

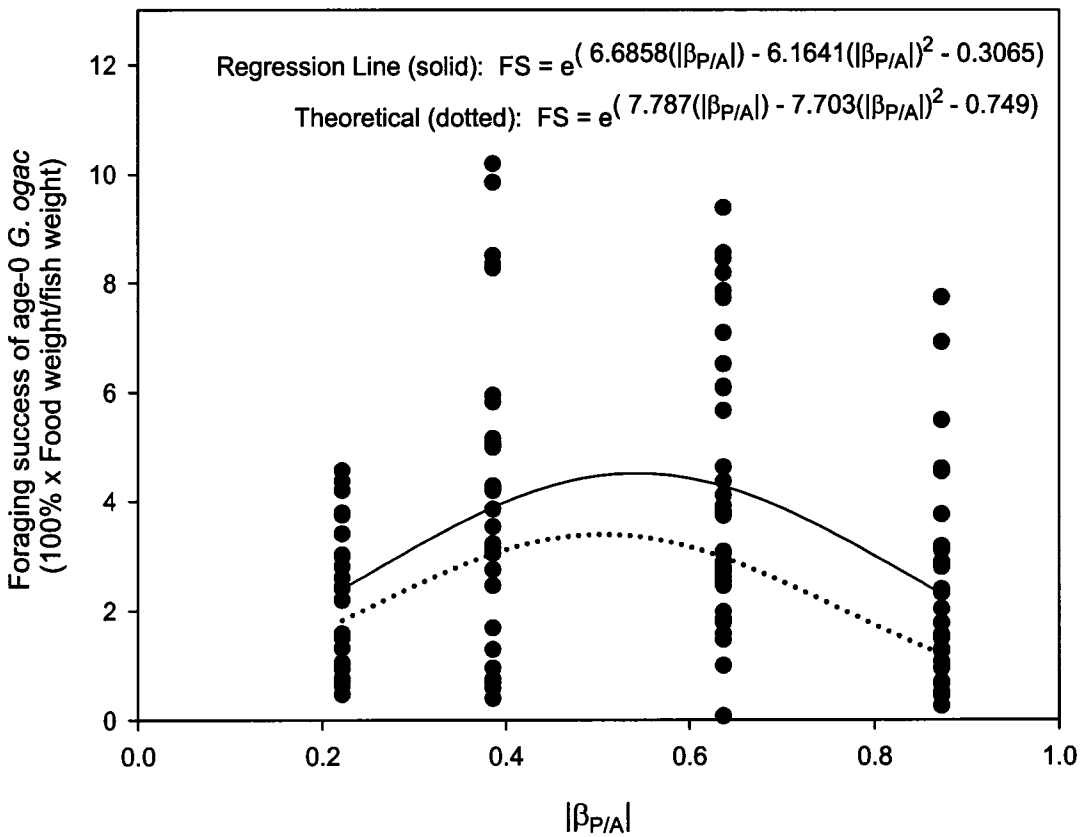
3.2 The relationship between age-0 Greenland cod (*G. ogac*) density (D) and individual age-0 Greenland cod foraging success (FS) in Newman Sound, Bonavista Bay.

3.3 The relationship between age-0 Greenland cod (*G. ogac*) foraging success (FS) and $|\beta_{P/A}|$ for both the theoretical prediction (dotted line) and the empirically derived regression (solid line).


MI
0.8370
Outer Newman Sound
Inner
Newman Sound
HC
0.3881
SB
0.9730
BB
0.2216
NEWFOUNDLAND


D = e (13.95|βP/A| - 13.78|βP/A|2 + 1.66)
Density of age-0 G. ogac (#/seine haul)
10000
1000
100
10
1
0.1
BB
HC
MI
SB
0.0
0.2
0.4
0.6
0.8
1.0
|βP/A|


D = e^1.789ln(FS+5.910)
Density of age-0 G. ogac (Natural log #/seine haul)
Foraging success of age-0 G. ogac (100% x Food weight/fish weight)
0
2
4
6
8
10
12
2
4
6
8


Regression Line (solid): FS = e(6.6858(|βP/A|) - 6.1641(|βP/A|)2 - 0.3065)
Theoretical (dotted): FS = e(7.787(|βP/A|) - 7.703(|βP/A|)2 - 0.749)
Foraging success of age-0 G. ogac
(100% x Food weight/fish weight)
0
2
4
6
8
10
12
0.0
0.2
0.4
0.6
0.8
1.0
|βP/A|

Chapter 4: Summary, Conclusions, and Further Work

My thesis illustrates that age-0 fish distribution in Newfoundland's nearshore waters during the month of September are influenced by the spatial arrangement of eelgrass, such that densities of Atlantic cod, Greenland cod, and white hake are highest at sites of intermediate spatial complexity. Furthermore, I have provided support for Wells' (2002) Intermediate Optimum Hypothesis, which states that eelgrass sites of intermediate complexity support the highest fish densities because they provide an optimal trade-off between foraging in open areas and evading predators via the use of protective cover. Using individual foraging success (determined by stomach fullness) as a measure of this trade-off, I have used a predictive model to show that at sites of intermediate complexity, age-0 Greenland cod forage most efficiently, whereas foraging success in continuous meadows or highly fragmented areas is reduced. In this thesis, I have addressed several important concepts to the study of animal-habitat interactions including scale of assessment, measurement of habitat spatial configuration, and species' responses to habitat fragmentation.

Historically, the concept of scale has been omitted from studies concerning the distribution or abundance of aquatic organisms with respect to habitat (Adams 1976a, Adams 1976b, Orth and Heck 1980, Orth *et al.* 1984, Gibson 1994, Miranda and Pugh 1997, Ross *et al.* 1997). However, the influence of scale on patterns in ecological systems in gaining recognition as researchers acknowledge that ecological processes may function differently at fine and broad resolutions (Wiens 1989). In Chapter 2, I demonstrated that the relation of age-0 juvenile Atlantic cod densities in Newman Sound with respect to

eelgrass perimeter length or area coverage varied with scale of assessment, and as such, single-scale analysis was insufficient to evaluate this influential, early-life history, habitat interaction. In addition, this result illustrated another concern with single-resolution analyses, because at coarse resolutions, the relationship between juvenile Atlantic cod density and eelgrass habitat was eliminated as a result of loss of information. In addition to difficulties in assessing scale-dependent relationships, conclusions drawn from single resolution assessments of the associations between juvenile cod and eelgrass may be biologically erroneous. Juvenile cod utilize eelgrass at a range of resolutions, extending from protective cover in patches to distribution on the scales of coves to coastlines. Additionally, the irregular pattern of eelgrass causes its measurement to be sensitive to scale. Therefore, addressing the association between age-0 fish and eelgrass pattern by integrating multiple-resolutions is biologically suitable, rather than determining an 'appropriate' single scale of investigation.

The use of multi-scale (fractal) measures to assess habitat patterning alleviates the concern that scale-dependent patterns might be assessed at an inappropriate resolution. In addition, such measures provide a numerical estimate of habitat quality that permit comparison among habitat types (McCoy and Bell 1991, Gee and Warwick 1994, Beck 1998, Beck 2000) and evaluation of their ecological significance to associated fauna. Despite these benefits of fractal measures, the results of Chapter 2 show that single measures of fractal complexity (D_P or D_A) are inadequate to describe the relationship between age-0 Atlantic cod density and eelgrass habitat configuration. Specifically, I demonstrated that, even if a significant relationship exists between cod density and

eelgrass perimeter convolution (D_P) or eelgrass area fragmentation (D_A) within a small geographical scale, the result cannot be extended to include larger expanses of coastline over which the eelgrass-cod interactions occur. Only a fractal measure that combines the influence of perimeter convolution and area fragmentation, $\beta_{P/A}$, yielded consistent and significant relationships between cod density and eelgrass habitat structure in both the small- and large-scale surveys. This is the first study that uses this method to assess habitat complexity, and therefore, also the first that uses it to describe changes in faunal density.

Recently, a large body of literature (e.g. Davidson 1998, Gustafson 1998, Bogaert 2003, Sleeman *et al.* 2005) has emerged that debates how to best quantify spatial heterogeneity. These studies cite problems in interpretation of indices as a hindrance to the dissemination and understanding of findings which concern faunal interactions with habitat structure. In general, it is important that the measure used is applicable to the system of study and correctly addresses the aspect of habitat hypothesized to be influential. Therefore, several measures may be appropriate for studying habitat heterogeneity. However, it is imperative to understand clearly how these measures reflect changes in habitat.

I have investigated how the fractal measure, $\beta_{P/A}$, responds to changes in its components D_P and D_A, and therefore this measure can be used with confidence. Furthermore, because $\beta_{P/A}$ describes habitat shape, it allows this poorly investigated, but potentially important, habitat feature to be further examined. Of course, eelgrass growth patterns are not true fractals, defined as a self-similar pattern across an infinite

mathematical set. However, fractal geometry provides a more realistic assessment of natural patterns, such as the irregular mode of eelgrass growth, than can be derived from Euclidean geometry alone. Therefore, fractal analysis can be a useful tool to describe habitat patterns such as eelgrass complexity, despite their finite nature and the fact that their self-similarity may be limited to a range of resolutions.

Irregular patterns of habitat can result from naturally convoluted growth, or by fragmentation. Eelgrass spatial pattern can be generated by both of these processes. Despite a great interest in the effects of fragmented habitat on resident fauna, surprisingly little work has investigated how the shape of fragmented habitat may influence the survival of its inhabitants. The results of Chapter 2 demonstrated that like Atlantic cod, the distribution of age-0 Greenland cod depends on the spatial configuration of eelgrass as measured by perimeter convolution and area fragmentation. In Chapter 3, I predicted and verified that foraging success, which may indicate a trade-off in feeding and predator avoidance, is also dependent upon the spatial configuration of eelgrass. Further research stemming from this investigation might uncover how the individual components of this trade-off respond to eelgrass fragmentation, controlling for such influences as differences in food availability, competitor density, and predator density.

Additionally, the results of my thesis shed some light on how three sympatric species, which appear to have similar habitat and foraging requirements, can coexist. It has been suggested that co-habitance of multiple similar species might be permitted, despite competition for the same resources and evasion from the same predators, through differences in how these species resolve their foraging/predation risk trade-offs. For

example, stomach content analysis of age-0 Greenland cod suggest a comparable diet to their congener, Atlantic cod, however differences in the foraging strategy of each are unknown. Greenland cod do rely more heavily on eelgrass than Atlantic cod (Laurel *et al.* 2003a). Therefore, given the reduced use of barren substrate, it is possible that Greenland cod rely more heavily on prey species closely associated with eelgrass plant structure, eelgrass edge habitat, or the isolated barren areas that are afforded by eelgrass sites of intermediate complexity. Also, age-0 Greenland cod predation risk is unknown. Linehan *et al.* (2001) and Laurel *et al.* (2003a) performed tethering experiments to assess predation risk of age-0 Greenland and Atlantic cod in vegetated and unvegetated substrates, but the results for the two species were not distinguished. It is important to realize that tethering rates reveal little about the difference in predation risk between species, as normal evasion tactics and mobility are impaired. The findings of my study highlight the fact that despite apparently similar ecologies, the habitat responses and requirements of even closely related species may differ substantially. Additionally, these studies reveal that further investigations of juvenile Greenland cod are required, because they may influence habitat use patterns of important ecological and economic species in nearshore Newfoundland waters.

Likewise, more research is required to fully elucidate the habitat use patterns of juvenile white hake and the underlying mechanisms that drive these patterns. To determine the validity of the observed parabolic relationship (Chapter 2), additional sampling is necessary, preferably over a larger spatial scale. Moreover, because white hake share nursery habitat with another economically important gadid in Newfoundland

waters, greater understanding of age-0 hake territoriality, site fidelity, nutritional requirements, and foraging behaviour is needed. Highly piscivorous as adults, hake species are well documented as important predators of commercial fish species. Therefore, it is possible that white hake affect such species earlier in their life-history than previously expected, their piscivorous ability as age-0s combined with competition for nursery habitat.

My thesis provides support for the postulated secondary critical survival period (Sissenwine 1984) in the early life history of Atlantic cod. Hjort's (1914) critical period concept suggests that year-class strength of marine fishes hatched from small eggs depends upon high mortality rates during the planktonic larval stage. Since the collapse of the Atlantic cod population in 1992, larval abundance has not been a reliable predictor of year-class strength (Anderson and Dalley 1997, Schneider *et al.* 1997), suggesting that a secondary mortality-sensitive period is operating. My thesis identifies that availability of appropriate nursery habitat can influence the density distribution and the success of juvenile cod. Moreover, I have demonstrated that the degree of fragmentation in a habitat – not simply the amount of habitat – may determine the ability for individuals to persist through this secondary mortality period. Furthermore, my thesis suggests that recovery and resilience of any species with depressed populations may be influenced by the spatial configuration of habitat, and therefore this factor should be considered when designating critical habitat in conservation and recovery efforts.

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